Alma Mater Studiorum – Università di Bologna

DOTTORATO DI RICERCA IN

Scienze ambientali: Tutela e Gestione delle Risorse Naturali

Ciclo XXIII

Settore/i scientifico-disciplinare/i di afferenza: BIO/07 Ecologia

Spatial and temporal variability and ecological processes in the epibenthic assemblages of the Northern Adriatic Sea

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Esame finale anno 2011

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Abstract della tesi di dottorato:

SPATIAL AND TEMPORAL VARIABILITY AND ECOLOGICAL PROCESSES IN THE EPIBENTHIC ASSEMBLAGES OF THE NORTHERN ADRIATIC SEA

Several coralligenous reefs occur in the soft bottoms of the northern Adriatic continental shelf. Mediterranean coralligenous habitats are characterised by high species diversity and are intrinsically valuable for their biological diversity and for the ecological processes they support. The conservation and management of these habitats require quantifying spatial and temporal variability of their benthic assemblages. This PhD thesis aims to give a relevant contribution to the knowledge of the structure and dynamics of the epibenthic assemblages on the coralligenous subtidal reefs occurring in the northern Adriatic Sea.

The epibenthic assemblages showed a spatial variation larger compared to temporal changes, with a temporal persistence of reef-forming organisms. Assemblages spatial heterogeneity has been related to morphological features and geographical location of the reefs, together with variation in the hydrological conditions.

Manipulative experiments help to understand the ecological processes structuring the benthic assemblages and maintaining their diversity. In this regards a short and long term experiment on colonization patterns of artificial substrata over a 3-year period has been performed in three reefs, corresponding to the three main types of assemblages detected in the previous study. The first colonisers, largely

depending by the different larval supply, played a key role in determining the heterogeneity of the assemblages in the early stage of colonisation. Lateral invasion, from the surrounding assemblages, was the driver in structuring the mature assemblages. These complex colonisation dynamics explained the high heterogeneity of the assemblages dwelling on the northern Adriatic biogenic reefs. The buildup of these coralligenous reefs mainly depends by the bioconstruction-erosion processes that has been analysed through a field experiment. Bioconstruction, largely due to serpulid polychaetes, prevailed on erosion processes and occurred at similar rates in all sites. Similarly, the total energy contents in the benthic communities do not differ among sites, despite being provided by different species. Therefore, we can hypothesise that both bioconstruction processes and energetic storage may be limited by the availability of resources. Finally the major contribution of the zoobenthos compared to the phytobenthos to the total energetic content of assemblages suggests that the energy flow in these benthic habitats is primarily supported by planktonic food web trough the filter feeding invertebrates.

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Chapter 1. General Introduction

1.1. Epibenthic assemblages of the northern Adriatic Sea coralligenous reefs

Mediterranean coralligenous habitats are biogenic reefs mainly built by encrusting calcareous algae growing in dim light condition (Ballesteros 2006). Subtidal coralligenous reefs occur all around the Mediterranean coast and are characterised by a variety of morphologies. These habitats are included among the most important Mediterranean "hot spot" of species diversity (Boudouresque 2004) and they are intrinsically valuable for the biological diversity and for the ecological processes they support. The complex structure of these biogenic reefs supports a variety of species assemblages dominated by living algae, borers, and vagile species inhabiting holes and crevices (Ballesteros 2006). Growth and structure of the coralligenous reefs is affected by several environmental factors as light, temperature, nutrient concentrations and hydrodynamics. Unfortunately, little is known about the complex interaction between environmental variables and the structure of the assemblages, and its variation at different spatial and temporal scale (Ballesteros 2006).

Coralligenous reefs occur also in the silty-sand sedimentary bottoms of the northern Adriatic continental shelf. These reefs were recorded in the 18th century (Olivi 1792) while the first underwater exploration, mainly regarding their origins and geological features, goes back to '60s (Stefanon 1969; Braga and Stefanon 1969). Studies on the benthic assemblages of the Adriatic biogenic reefs started in the '90s, and only scattered descriptive data on few reefs are available.

Quantify spatial and temporal variability of the benthic assemblages is required for an appropriate management and for the conservation of the coralligenous habitats. Understanding patterns of variation can increase the precision of ecological predictions regarding, for example, the effectiveness of conservation strategies or the consequences of natural and anthropogenic disturbances (Levin 1992; Benedetti-Cecchi et al. 2000).

1.2 Recruitment processes and their role in structuring the epibenthic assemblages

Recruitment process in marine invertebrates entails different stages: larval dispersal, search of suitable substratum, aided by chemical and physical cues and settlement, in the case of sessile invertebrates attachment to the substratum, and metamorphosis when the animal becomes a juvenile and looks like a small adult (Keough and Downes 1982). Patterns of specie distribution in sessile marine invertebrates are controlled by several important factors: i) planktonic events (i.e. larval supplies, dispersal capability, mortality, etc.); ii) active larval choices during settlement, generally affected by water characteristics close to the substratum, larval behaviour, pre-emption of surface space, etc.; and iii) juveniles post-settlement mortality mainly due to biological interactions (Connell 1985).

Species distribution and abundance in benthic assemblages is strongly influenced by settlement and recruitment processes (Downes and Keough 1998) which change in relation to several biological and physical parameters operating over a range of temporal and spatial scale (Turner and Todd 1993). Regional recruitment variability mainly results from broad-scale hydrodynamics processes and shoreline configuration; while local variability is mainly affected by micro-scale heterogeneity, biotic interaction

and larval supply and behaviour. Quantifying regional and local spatial variability of recruitment could be useful to understand the structure of the assemblages and their temporal differentiation. The use of artificial substrata to carry out studies on the role of recruitment in structuring the assemblages, can be useful to minimize the influence of the habitat heterogeneity (Smith and Rule 2002; Glasby 1998).

1.3 Bioconstruction-erosion processes in coralligenous reefs

Biogenic reefs are built by the accumulation and cementation of calcareous skeleton of many marine organisms and other particles. These formations are very dynamic, involving accretion due to skeletal growth, biotic interaction among co-occurring species, and erosion due to physical and biological processes. They are very complex systems in term of physical structure, associated biota and ecological processes they support (Cocito 2004).

Biogenic carbonate structures assume an important ecological role especially in the northern Adriatic silty-sandy bottoms where they provide 'island' of hard substrate for the colonisation by benthic species, increasing habitat complexity and species diversity (Jones et al. 1994). Persistence of these biogenic structures depends on the interplay of the bioconstruction-erosion processes. The influence of both bioconstruction and bioerosion on carbonate budget and their dynamics have been extensively studied in coral reef environments (e.g.: Smith and Kinsey 1978); Le Campion-Alsumard et al. 1993). On the other hand, in Mediterranean coastal marine environments, where calcareous algae thrive and dominate in a large range of habitats (Canals and Ballesteros 1997; Cebrian et al. 2000; Garrabou and Ballesteros 2000), little is known about their potential role as bioconstructors. In the north-western Mediterranean Sea, few studies

on carbonate content and production in benthic ecosystems have been carried out (Canals and Ballesteros 1997, Cebrian et al. 2000), and a better understanding of the role of macrophytobenthos and macrofauna in the carbon budget is needed.

1.4 Possible species responses to environmental changes

Marine biodiversity and ecosystems are responding to global climate change that involves global warming, reduction of seawater pH, sea level rise, increase of storms and extreme events frequency, occurring to both regional and local-scale (IPCC 2007). Moreover, direct responses of biodiversity to global climate-driven change are superimposed to several smaller-scale processes (Hawkins et al. 2009). Due to global climate change and related issues, rapid variations are occurring in the distribution patterns of rocky intertidal species on a European scale ({Hawkins, Sugden, et al. 2009 #44280}). Historical data analyses suggest that southern species are advancing while northern species are likely retreating along the latitudinal gradient (Helmuth et al. 2006). In the Mediterranean and Black Sea, changes in the distribution of marine species are already observed (e.g.: Astraldi et al. 1995; Garrabou et al. 2009) and much more are expected for the forthcoming years (Bianchi 2007; Sezgin et al. 2010).

The geographical distribution of the benthic species living on the northern Adriatic biogenic reefs could be related to some environmental conditions (i.e. light, temperature, salinity, sedimentation rate, etc.) that are involved in structuring and maintaining the species diversity of these coralligenous assemblages (Ponti et al. 2011). The increased frequency of the summer thermocline deepening, due to climatic anomalies, and the consequent thermal stress, raise questions about the possible response of several species. Among them, the zooxanthellate octocoral *Maasella*

edwarsi (De Lacaze-Duthiers 1888), which is present in only one of the several investigated reefs with a dense population, could be one of the most sensitive species.

Aims of the thesis

The first study of this thesis quantified the spatial variability of the northern Adriatic coralligenous assemblages and identified the major environmental factors shaping the observed patterns of distribution.

The second study focused on role of the settlement and recruitment processes in structuring the assemblages and maintaining their diversity, including either local and regional scales as well as short and long-term analysis.

The third study dealt with the analysis of the balance between bioconstruction and erosion processes occurring in the northern Adriatic coralligenous reefs. The study was carried out using calcareous tiles, which allowed to disentangle the role of endobionts and sessile and vagile epibionts.

Finally, a preliminary study on the responses of the zooxanthellate octocoral *Maasella edwarsi* (De Lacaze-Duthiers 1888) to increasing temperature were carried out in order improve our knowledge on possible future scenarios in relation to global climate change.

Chapter 2. Manuscripts

Manuscript 1. Spatial-temporal variability of epibenthic assemblages on subtidal biogenic reefs in the northern Adriatic Sea

Introduction

Mediterranean coralligenous concretions are biogenic reefs formed mainly by the accumulation of calcareous encrusting algae growing in dim light conditions (*sensu* Ballesteros 2006). Their structure is shaped by the growth patterns of dominant algal species, together with lithification and erosion processes. Coralligenous reefs occur between 20 and 120 m in depth along the Mediterranean coast (Laborel 1987). Coralligenous rims grow on coastal rocks (e.g. vertical cliffs, overhangs and outer part of marine caves) while platform banks develop on the continental shelves over consolidated sediments, coalesced rhodoliths or pre-existing rocky outcrops (Laborel 1987). The latter generally presents biogenic flat reefs with a thickness varying from 0.5 to 4 m, often surrounded by sedimentary bottoms (Ballesteros 2006). Coralligenous assemblages include algal and animal builders, bioeroders, several epi- and endo-faunal species; moreover, they host a rich cryptofauna (Hong 1982). These habitats are considered a "hot spot" of species diversity in the Mediterranean sea (Boudouresque 2004), therefore these reefs are intrinsically valuable for their biological diversity and for the ecological processes that they can support (Ballesteros 2006). Mediterranean coralligenous assemblages are threatened by several sources of human disturbance (e.g. pollution, sediment deposition, recreational fishing and trawling, diving) (Hong 1983; Garrabou et al. 1998; Airoldi 2003 and reference therein; Balata et al. 2005). Global environmental changes, leading to mass mortality events (Cerrano et al. 2000; Linares et al. 2005; Garrabou et al. 2009) and invasions by alien species (Occhipinti-Ambrogi

2007; Piazzi and Balata 2009), are an additional source of disturbance to these habitats. Other important causes of mortality for these benthic assemblages are bottom hypoxia/anoxia events (Ott 1992; Kollmann and Stachowitsch 2001; Zuschin and Stachowitsch 2009 and references therein), and suffocation by mucilaginous aggregates (Molin et al. 1992; Russo et al. 2005 and references therein). Both phenomena periodically happen in the northern Adriatic Sea.

Conservation and management of the Mediterranean coralligenous habitats require to quantify patterns of variability of the benthic assemblages at a range of spatial and temporal scales (Garrabou et al. 1998; Ferdeghini et al. 2000; Piazzi et al. 2002; Piazzi et al. 2004; Balata et al. 2006; Virgilio et al. 2006). Several studies have recently investigated spatial variability of coralligenous assemblages on coastal rocky cliffs, while structure and variability of platform banks have been rarely investigated.

Although northern Adriatic platform banks were firstly mentioned in the 18th century (Olivi 1792), to date, their benthic assemblages has been analysed only in few locations (Brunetti 1994; Gabriele et al. 1999; Mizzan 2000; Molin et al. 2003; Soresi et al. 2004) and their spatial and temporal variability remains little known (Fava et al. 2009a, Fava et al. 2009b). An approximate checklist of the benthic organisms living on these outcrops can be found in Casellato and Stefanon (2008).

The aim of this study was to investigate spatial and temporal variability of the species assemblages on the coralligenous reefs of the northern Adriatic platform at regional scale throughout four years. Moreover, possible correlations of the species assemblages with environmental variables, geo-morphological features and habitat complexity, were investigated.

Materials and methods

Study area

Coralligenous biogenic reefs of the northern Adriatic continental shelf, range from a few to several thousands square metres in size, and up to 4 metres in height from surrounding bottoms (Newton and Stefanon 1975). In the present study, 26 coralligenous reefs, locally named 'tegnùe', scattered over an area of about 500 km^2, at a depth ranging between 18 and 30 m, and distant 6 to 24 km from the coast, were investigated (Fig. 1). Each outcrop was labelled in accordance with previous publications (e.g. Ponti and Mescalchin, 2008; Fava et al. 2009a). The sedimentary bottoms surrounding the outcrops were mainly characterised by terrigenous sediments superimposed to the Würmian glaciation continental deposits (10-7,000 years ago; Trincardi et al. 1994). Sea currents in the area are driven by the cyclonic geostrophic circulation and by its summertime baroclinic component (Artegiani et al. 1997a, Artegiani et al. 1997b). A strong seasonal halocline and thermocline are found in the area; light penetration to the bottom was strongly affected by fluvial runoff, current transport of sediments, and phytoplankton blooms (Bernardi Aubry et al. 2004 and references therein). Measures carried out in two stations at 25 m in depth indicated an irradiance of about 30-150 MJ m^{-2} yr^{-1} (Franco 1984), corresponding to a light attenuation of 1-2% of the mean surface irradiance, estimated in 5,800 MJ m^{-2} yr^{-1} (Bernardi Aubry et al. 2004).

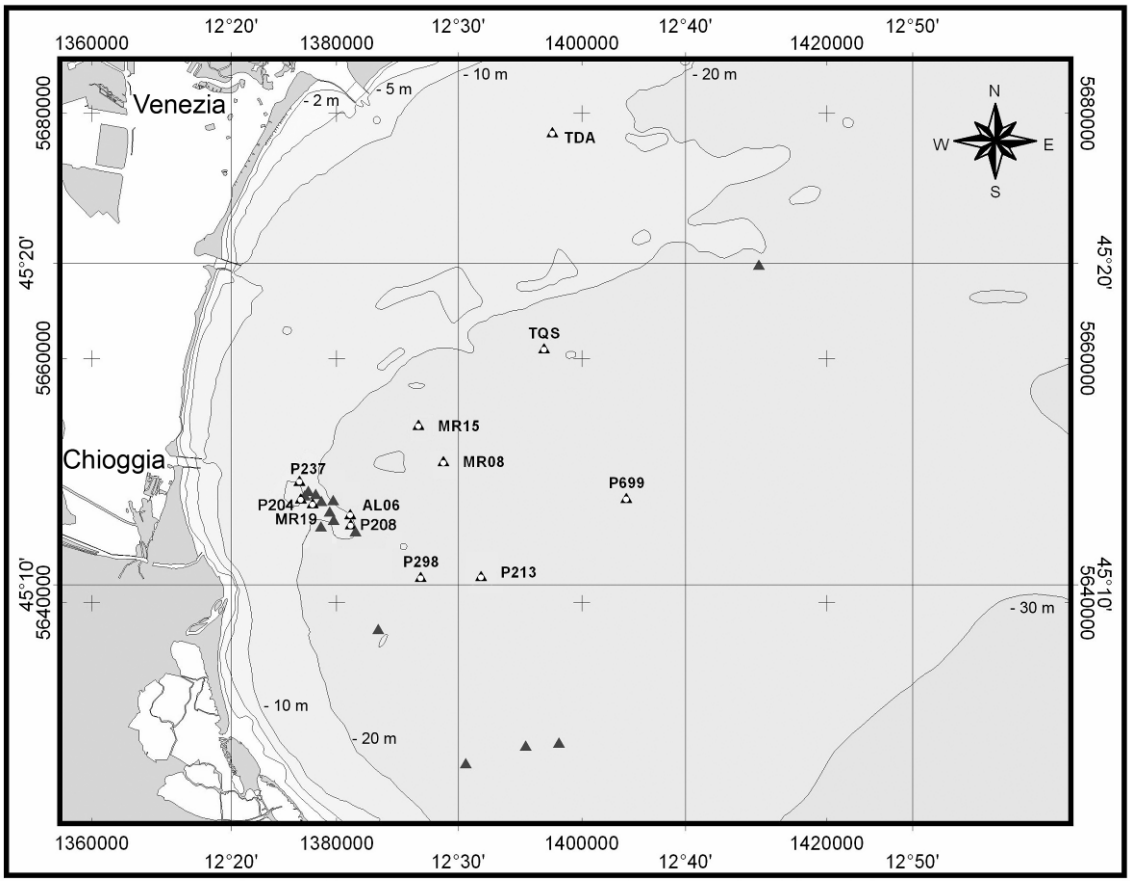


Fig. 1. Map of study area, showing the explored rocky outcrops and the twelve randomly selected sampling sites (projection grid utm33 wgs84).

Table 1. Location (geographic coordinates, datum wgs84), geo-morphological features (depth, distance from the coast, extent and height of relief, habitat complexity), surrounding sediment and water characteristics (mud (i.e. silt + clay), organic matter, mean temperature and salinity) of the study sites.

Site	Lat N	Lon E	Depth	Coast Dist.	Extent	Height	Habitat complexity	Mud	Organic matter	Mean T Aug	Mean T (Jun-Aug)	Mean S (Jun-Aug)
			(m)	(km)	(m^2)	(m)		(%)	(% LOI)	°C	°C	(psu)
AL06	45° 12.188'	12° 25.258'	21.9	8.5	27,759	2.1	109.98	26.48	4.46	24.11	21.63	37.79
MR08	45° 13.831'	12° 29.354'	22.2	14.6	2,096	1.5	64.13	7.76	4.98	23.54	21.18	37.90
MR15	45° 14.978'	12° 28.258'	23.3	13.6	400	1.5	29.74	22.54	3.24	23.88	21.42	37.84
MR19	45° 12.519'	12° 23.598'	21.1	7.0	441,917	1.5	120.59	22.1	6.06	24.88	22.46	37.52
P204	45° 12.674'	12° 23.076'	20.2	6.6	276,297	2.2	234.54	38.79	4.46	24.88	22.45	37.52
P208	45° 11.877'	12° 25.260'	23.0	8.3	2,380	1.5	49.35	19.91	4.53	24.11	21.62	37.80
P213	45° 10.270'	12° 31.013'	25.4	15.0	1,288	1.2	44.70	19.37	1.82	23.09	20.86	37.95
P237	45° 13.218'	12° 23.020'	20.7	6.8	9,634	4.2	154.30	48.15	4.82	25.07	22.68	37.44
P298	45° 10.240'	12° 28.354'	24.3	11.5	489	0.8	18.47	32.34	3.34	23.02	20.74	37.98
P699	45° 12.683'	12° 37.406'	27.0	23.9	900	0.8	12.45	21.84	4.63	22.24	20.25	38.05
TDA	45° 24.040'	12° 34.150'	19.4	7.5	1,600	3.7	153.18	6.98	5.94	25.17	22.94	37.39
TQS	45° 17.355'	12° 33.792'	23.4	19.5	375	0.8	15.93	24.59	3.65	24.21	21.66	37.81

Sampling and laboratory analyses

Composition and abundances of the epibenthic assemblages were investigated annually, using a non-destructive photographic sampling method, on 12 randomly selected sites located on separated rocky outcrops some kilometres apart (Fig. 1 and Table 1). Photographic samples (17.0x22.6 cm, 0.0384 m^2) were collected from 2003 to 2006 in August, using an Olympus Cammedia C-7070 WZ underwater digital camera (7 Mpixel) equipped with a TTL strobe and two 50 Watt halogen lights. A rigid spacer connected to the camera guaranteed constant distance and parallelism between focal plane and substrata. Ten random photo-quadrates were analysed at each sites for each sampling date. This photographic method could underestimate the abundance of some species, like the coralline algae, sometimes partially hidden by other organisms, but it has been widely used in study dealing with spatial and temporal variability of hard bottoms epibenthic assemblages because it allowed large-scale high replicated investigations (Bianchi et al. 2004). Sampling area and number of replicates were defined based on the size of the species occurring on the outcrops and in accordance with the methodologies commonly used on the Mediterranean hard bottoms (Bianchi et al. 2004). Species reference collection over the 26 investigated outcrops (Fig 1), was created by collecting voucher specimens, corresponding to field photographs collection, to allow the identification of the organisms to the lowest possible taxonomic level. Percent cover of sessile organisms was quantified by superimposing a grid of 100 equal sized squares and identifying all taxa visible within each quarters of these squares, i.e. ± 0.25% (Meese and Tomich 1992; Dethier et al. 1993). Percent cover was related to the total readable area of each image, obtained subtracting dark and blurred zone or portion covered by motile organisms. Organisms were identified in accordance with the species reference collection, and assigned to morphological and ecological groups. The

endolithic bioeroder bivalve *Gastrochaena dubia* was identified and quantified by counting the siphon holes.

Location and morphology of each sampling site was obtained by DGPS and single beam sonar survey, which allowed the 3D GIS based mapping. Habitat complexity (Hci) was estimated linearly combining the rugosity index, height and extent of relief. The rugosity index was estimated as mean ratio between the contoured and straight length among two points (Brokovich et al. 2006) on a 10 metres cross section of the outcrop carried out from the digital bathymetries, replicated six time for each site.

Sediment samples were collected close to the outcrops. Sand and silt-clay content was measured as dry weight percentage after wet sieving (0.063 mm mesh), retaining the fine fraction by filter paper (particle retention 11μm), and drying at 90°C for 24 hours. Sediment organic content was determined as percent loss of weight of the dried samples at 90°C for 24 hours, after ignition (% *LOI*) at 500°C for 8 hours (King et al. 1998).

Hydrographical data were not available for the area, mean daily temperature (°C) and salinity (psu) near the bottom at each sampling site and for the whole study period were estimated using the ASHELF model. ASHELF is a numeric model developed within the ADRICOSM project (http://gnoo.bo.ingv.it/adricosm/), based on the Princeton Ocean Model (Zavatarelli and Pinardi 2003 and references therein) with data assimilation for the northern Adriatic basin with a 1.5 km grid.

Data analyses

Epibenthic assemblages were analysed in terms of percent cover. Species richness (number of taxa, *S*), species diversity (as Hill's diversity number *N1* = Exp *H'*,

where *H'* is the Shannon's index) and the corresponding evenness component (as *N10* = *N1*/*S*) were calculated for each replicate sample (Gray 2000). Two-way analysis of variance (ANOVA) was applied to single taxon and to diversity indices to test for differences among years (4 levels, random) and sites (12 levels, random). The homogeneity of variances was assessed by Cochran's C test and data were transformed if required. Only when data were distinctly binomially distributed, the arc-sin transformation was applied (Underwood 1997). Percentages of variance components (VC%) were calculated in order to estimate the magnitude of the variability attributable to spatial and temporal factors in comparison to the residual variations among replicates (Underwood 1997).

Spatial distribution and temporal variation of the assemblages were analysed using both principal coordinate analysis (PCO, i.e. metric multidimensional scaling) and cluster analysis (complete linkage method) based on Bray-Curtis similarity of square root transformed data (Gower, 1966; Clarke 1993). Each sampling site was represented on the PCO bi-dimensional ordination plot by the centroid of 10 replicates. Distance-based two-way permutational multivariate analysis of variance (PERMANOVA; Anderson 2001; Anderson and ter Braak 2003) was used to test for differences of epibenthic assemblages among the investigated years (4 levels, random) and sites (12 levels, random). The analysis was based on Bray-Curtis dissimilarities on squared root transformed data. Percentages of variance component (VC%) were calculated for each terms of the analysis.

Relationship between the similarity patterns of the assemblages and environmental variables were investigated by multivariate multiple regression using the DISTLM forward procedure that provided a selection of variables that better explain the observed patterns (McArdle and Anderson 2001). The selected environmental variables

were extent (Log_{10} transformed) and height of relief, depth, habitat complexity, distance from coast, longitude and latitude (UTM33 wgs84 coordinates), sediment mud (% silt + % clay) and organic matter (% *LOI*) content in the surrounding seabed, mean bottom temperature and salinity in August and during the summer (June-August) each year.

Possible linear correlations among the most abundant species percent cover and diversity indices with the environmental variables that better explain the assemblage's similarity patterns have been investigated by linear regression. The probability that the fitting line slope differed from zero was investigated by ANOVA.

Results

Flora and Fauna

The epibenthic assemblages found on the investigated northern Adriatic coralligenous reefs were very heterogeneous in terms of percent cover of the most abundant taxa. The assemblages were characterised by algal turf (percent cover between 2.7% and 61.37%), calcareous red algae (0.2%-52.35%), encrusting sponges (0.07%-20.28%), massive sponges (0.07%-25.31%), boring sponges (0%-25.44%), colonial ascidians (0%-18.23%), tubular sponges (0%-9.5%), zoantharians (0%-22.8%).

The dominant reef-forming organisms were encrusting calcareous red algae that mostly consisted of *Lithophyllum stictaeformae* (Areschoug in J. Agardh) Hauck, 1978, *Lithothamnion minervae* Basso, 1995 and *Peyssonnelia polymorpha* (Zanardini) F. Schmitz, 1879, while other uncalcified red algae included *Halymenia floresii* (Clemente y Rubio) C. Agardh, 1817 and *Botryocladia botryoides* (Wulfen) Feldmann, 1941. Algal turf was mainly composed by the Rodophyta *Polysiphonia* sp., *Antithamnion* sp. and *Rhodymenia* sp. and by the Chlorophyta *Cladophora* sp. and *Chaetomorpha* sp. The main bioeroders were the boring sponges *Cliona celata* Grant,1826, *Cliona rhodensis*

Rützler & Bromley, 1981, *Cliona thoosina* Topsent, 1887, *Cliona viridis* (Schmidt, 1862), *Pione vastifica* (Hancock, 1849) and the endolithic bivalve *Gastrochaena dubia* (Pennant, 1777). In terms of trophic guilds, epibenthic invertebrates included filter feeders, among which the most common were the sponges *Antho* (*Antho*) *inconstans* (Topsent, 1925), *Dictyonella incisa* (Schmidt, 1880), *Dysidea avara* (Schmidt, 1862), *Phorbas fictitius* (Bowerbank, 1866), *Mycale* (*Mycale*) *massa* (Schmidt, 1862), *Tedania* (*Tedania*) *anhelans* (Lieberkühn, 1859), the zoantharian *Epizoanthus* spp. and the ascidian *Polycitor adriaticus* (Drasche, 1883). The most common species are described in Ponti and Mescalchin (2008). The species checklist included 14 new records for the northern Adriatic Sea (see Appendix).

Species spatial distribution and temporal variability

Overall, the percent cover of calcareous algae (Fig. 2a), boring sponges (Fig. 2b), massive sponges, cnidarians and colonial ascidians showed clear spatial distribution patterns with significant differences among sites, while these groups appeared quite steady in time (ANOVA Site: $P < 0.01$; Table 2). The magnitudes of the variability among sites were similar or lower than the residual variations among replicates, indicating a high heterogeneity at local spatial scale. The abundance of non-calcareous algae (including algal turf), algal turf (Fig. 2c) and encrusting sponges showed complex site-specific temporal trends. Their differences among sites varied annually (ANOVA Year x Site: $P < 0.01$; Table 2), even if most of the observed variability was associated to differences among sites and replicates.

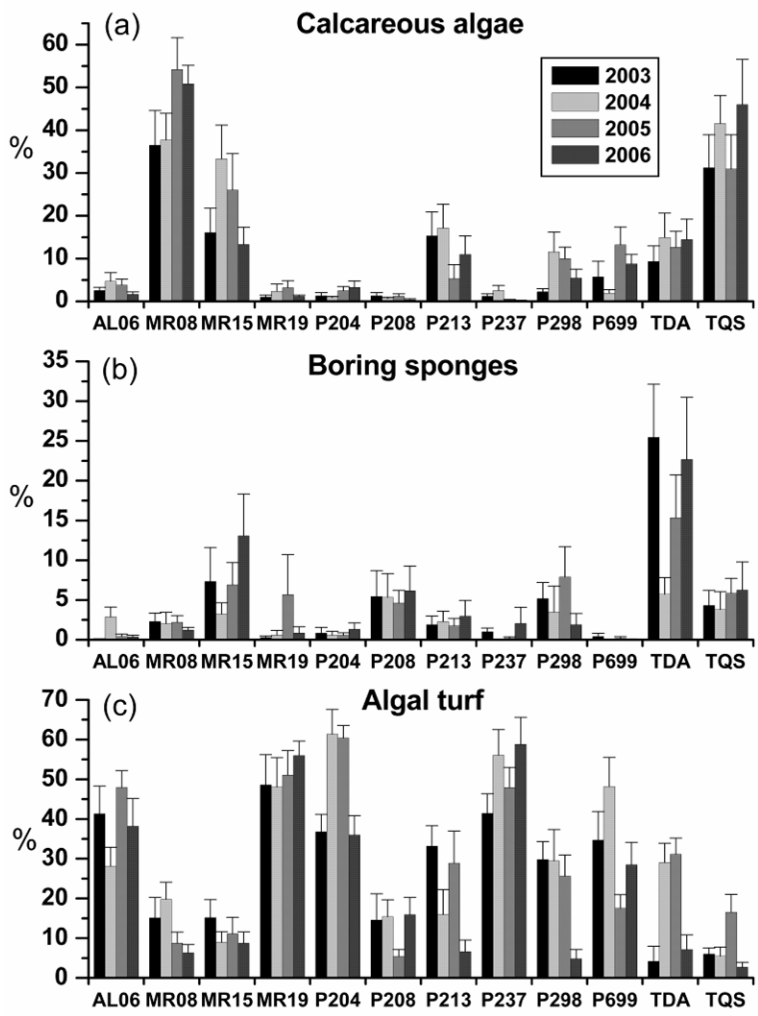


Fig. 2. Spatial and temporal trends of some ecological group: a) calcareous algae, b) boring sponges, c) algal turf (mean values ± SE).

Table 2. Results from ANOVA on epibenthic percent cover data of the most important ecological groups (VC% = percentage of variance components).

		Calcareous algae				Non calcareous algae				Algal turf				Encrusting sponges				
Source	**DF**	**MS**	**F**	***P***	**VC%**	**MS**	**F**	***P***	**VC%**	**MS**	**F**	***P***	**VC%**	**MS**	**F**	***P***	**VC%**	**F ver.**
Year (Y)	3	5.595	1.83	0.1611	0.39	1,149.230	1.09	0.3671	0.13	1,522.647	1.76	0.1748	0.96	2.514	0.63	0.5991	0.00	Y x S
Site (S)	11	118.556	38.75	0.0000	53.09	12,083.890	11.46	0.0000	44.38	10,785.860	12.44	0.0000	43.55	25.511	6.42	0.0000	18.18	Y x S
Y x S	33	3.060	1.24	0.1751	1.08	1,054.716	3.97	0.0000	12.69	867.067	3.40	0.0000	10.75	3.972	1.76	0.0065	5.81	RES
Res	432	2.471			45.44	265.949			42.80	254.752			44.74	2.251			76.01	
Transf.		Sqrt(x+1)				None				None				Sqrt(x+1)				

		Boring sponges				Massive sponges				Cnidarians				Colonial ascidians				
Source	**DF**	**MS**	**F**	***P***	**VC%**	**MS**	**F**	***P***	**VC%**	**MS**	**F**	***P***	**VC%**	**MS**	**F**	***P***	**VC%**	**F ver.**
Year (Y)	3	1.305	1.56	0.2171	0.30	7.374	2.79	0.0559	1.17	0.902	1.19	0.3275	0.14	0.336	0.26	0.8518	0.00	Y x S
Site (S)	11	13.547	16.22	0.0000	24.28	33.474	12.66	0.0000	22.83	10.793	14.27	0.0000	29.56	12.909	10.08	0.0000	22.89	Y x S
Y x S	33	0.835	0.85	0.7135	0.00	2.644	1.03	0.4196	0.25	0.756	1.31	0.1241	2.09	1.280	1.35	0.0955	2.63	RES
Res	432	0.987			75.42	2.558			75.75	0.579			68.21	0.946			74.48	
Transf.		Ln(x+1)				Sqrt(x+1)				Ln(x+1)				Ln(x+1)				

Analysing the most abundant epibenthic species individually, the percent cover of the calcareous algae *Lithothamnion minervae* did not vary in time but differed among sites, dominating the deepest locations (Table 3). Most of the variability of *L. minervae* was due to variations among replicates, rather than to the difference among sites.

Table 3. Results from ANOVA on epibenthic percent cover data of the most abundant species (VC% = percentage of variance components).

		Lithothamnion minervae				***Dictyonella incisa***				***Antho incostans***				
Source	**DF**	**MS**	**F**	***P***	**VC%**	**MS**	**F**	***P***	**VC%**	**MS**	**F**	***P***	**VC%**	**F ver.**
Year (Y)	3	667.936	2.46	0.0804	0.00	2.731	3.22	0.0353	1.29	4.246	3.09	0.0402	1.96	Y x S
Site (S)	11	8,842.842	8.87	0.0000	0.35	21.482	25.29	0.0000	42.30	10.113	7.37	0.0000	17.93	Y x S
Y x S	33	2,991.503	0.95	0.5558	0.00	0.849	1.27	0.1513	1.47	1.373	1.47	0.0472	3.62	RES
Res	432	41,380.990	2.46		99.65	0.670			54.94	0.932			76.48	
Transf.		ArcSin(%)				Ln(x+1)				Ln(x+1)				

		Cliona viridis				***Gastrochaena dubia***				***Polycitor adriaticus***				
Source	**DF**	**MS**	**F**	***P***	**VC%**	**MS**	**F**	***P***	**VC%**	**MS**	**F**	***P***	**VC%**	**F ver.**
Year (Y)	3	1.596	1.67	0.1914	0.42	36.306	15.2	0.0000	19.26	0.323	0.31	0.8203	0.00	Y x S
Site (S)	11	13.562	14.24	0.0000	24.77	13.016	5.45	0.0001	18.11	11.963	11.35	0.0000	23.93	Y x S
Y x S	33	0.953	1.00	0.4693	0.01	2.388	3.16	0.0000	11.12	1.054	1.25	0.1694	1.83	RES
Res	432	0.952			74.80	0.756			51.51	0.846			74.24	
Transf.		Ln(x+1)				Ln(x+1)				Ln(x+1)				

The abundance of the encrusting sponges *Dictyonella incisa* and *Antho* (*Antho*) *incostans* differed among sites. The first sponge exhibited a slightly decreasing temporal trend and appeared abundant in shallower and wider outcrops near the coast (Table 3); the second showed a higher spatial-temporal heterogeneity and a general increasing trend with depth (Table 3). The boring sponge *Cliona viridis* showed a site-specific distribution with a high abundance in some small outcrops, in particular in the site TDA, located off the Venice town (Table 3). The colonial ascidian *Polycitor adriaticus* was characterized by not significant variation among years and by high spatial heterogeneity with higher abundance in small and deep outcrops far from the coast (Table 3). These four species showed most of their variability associated to the

sites and to the variation among replicates, indicating a greater importance of spatial variability compared to the temporal changes.

The abundance of the endolithic bivalve *Gastrochaena dubia* showed an extremely high variability in both space and time (Table 3).

Species richness (*S*), species diversity (*N1*) and evenness (*N10*) showed high significant differences in the interaction Year X Site confirming the great spatial and temporal heterogeneity of the assemblages (Table 4). In particular, at all sites the number of species seemed to follow a common decreasing temporal trend during the first two years, and a subsequent increase.

Table 4. Results from ANOVA on species diversity indices (VC% = percentage of variance components).

		S				***N1***				***N10***				
Source	**DF**	**MS**	**F**	***P***	**VC%**	**MS**	**F**	***P***	**VC%**	**MS**	**F**	***P***	**VC%**	**F ver.**
Year (Y)	3	48.424	5.19	0.0048	7.25	2.852	0.700	0.5615	0.00	0.154	4.71	0.0076	3.96	Y x S
Site (S)	11	32.287	3.46	0.0028	12.78	19.835	4.840	0.0002	18.50	0.195	5.95	0.0000	15.91	Y x S
Y x S	33	9.329	3.16	0.0000	14.19	4.102	2.790	0.0000	12.39	0.033	1.70	0.0101	5.50	RES
Res	432	2.954			65.77	1.469			69.11	0.019			74.63	
Transf.		None				None				None				

Spatial-temporal variability of the epibenthic assemblages

Epibenthic assemblages showed a high variability in terms of both space and time, as showed by the PCO ordination plot (Fig. 3a). The first two axes of the PCO explained 44.4% and 12.0% of the variability of epibenthic assemblages, respectively. The scatter plot discriminated the assemblages inhabiting different sites, as confirmed by PERMANOVA showing significant interaction between Year and Site (Table 5). In addition, variability among sites was greater compared to the temporal changes as showed by the percentages of the variance components (Table 5). The cluster analysis detected five main groups of assemblages represented by: i) four outcrops located near

the shore (AL06, MR19, P204, P237); ii) three small outcrops quite far from the coast (MR08, MR15, TQS); iii) three south-eastern outcrops (P213, P298, P699) and the site TDA in August 2004 and 2005; iv) the site TDA in August 2003 and 2006; v) the site P208 alone (Fig. 3a). These clusters seemed to reflect the geographical position of the outcrops. Similarity of the assemblages among years within each site were generally higher than the similarity among sites in the same year, therefore patterns of similarity were driven by spatial rather then temporal variability (Fig. 3a).

Table 5. Results from PERMANOVA on Bray-Curtis dissimilarities of square rout-transformed epibenthic percent cover data (VC% = percentage of variance components).

Source	df	SS	MS	Pseudo-F	*P* (perm)	Unique perms	VC%
Year (Y)	3	35,886	11962	3.2911	0.0001	9,876	2.64 %
Site (S)	11	358,100	32555	8.9567	0.0001	9,850	27.51 %
Y x S	33	119,950	3634.7	2.2224	0.0001	9,655	7.61 %
Res	432	706,530	1635.5				62.24 %
Total	479	1,220,500					

Table 6. Multivariate multiple regression (DISTLM forward procedure) between epibenthic assemblages similarity pattern and environmental variable.

Variable	SS(trace)	Pseudo-F	*P*	Prop.	Cumul.
Extent (Log10) of relief	12,923	15.4530	0.0002	0.2515	0.2515
Distance from coast	4,882	7.2833	0.0002	0.0950	0.3465
Depth	4,093	5.3576	0.0002	0.0796	0.4261
Height of relief	3,612	6.0013	0.0002	0.0703	0.4964
Longitude	2,332	4.1580	0.0002	0.0454	0.5418
Mud (% silt + clay)	2,056	3.9218	0.0002	0.0400	0.5818
Temp. in August	1,825	4.0867	0.0002	0.0355	0.6173
Organic matter (% LOI)	1,375	2.7330	0.0022	0.0267	0.6440
Mean Temp. (June-August)	1,323	2.7457	0.0018	0.0257	0.6698
Mean Salinity (June-August)	1,227	2.8843	0.0010	0.0239	0.6937
Habitat complexity	1,212	3.2537	0.0006	0.0236	0.7172
Latitude	1,028	2.5135	0.0046	0.0200	0.7372

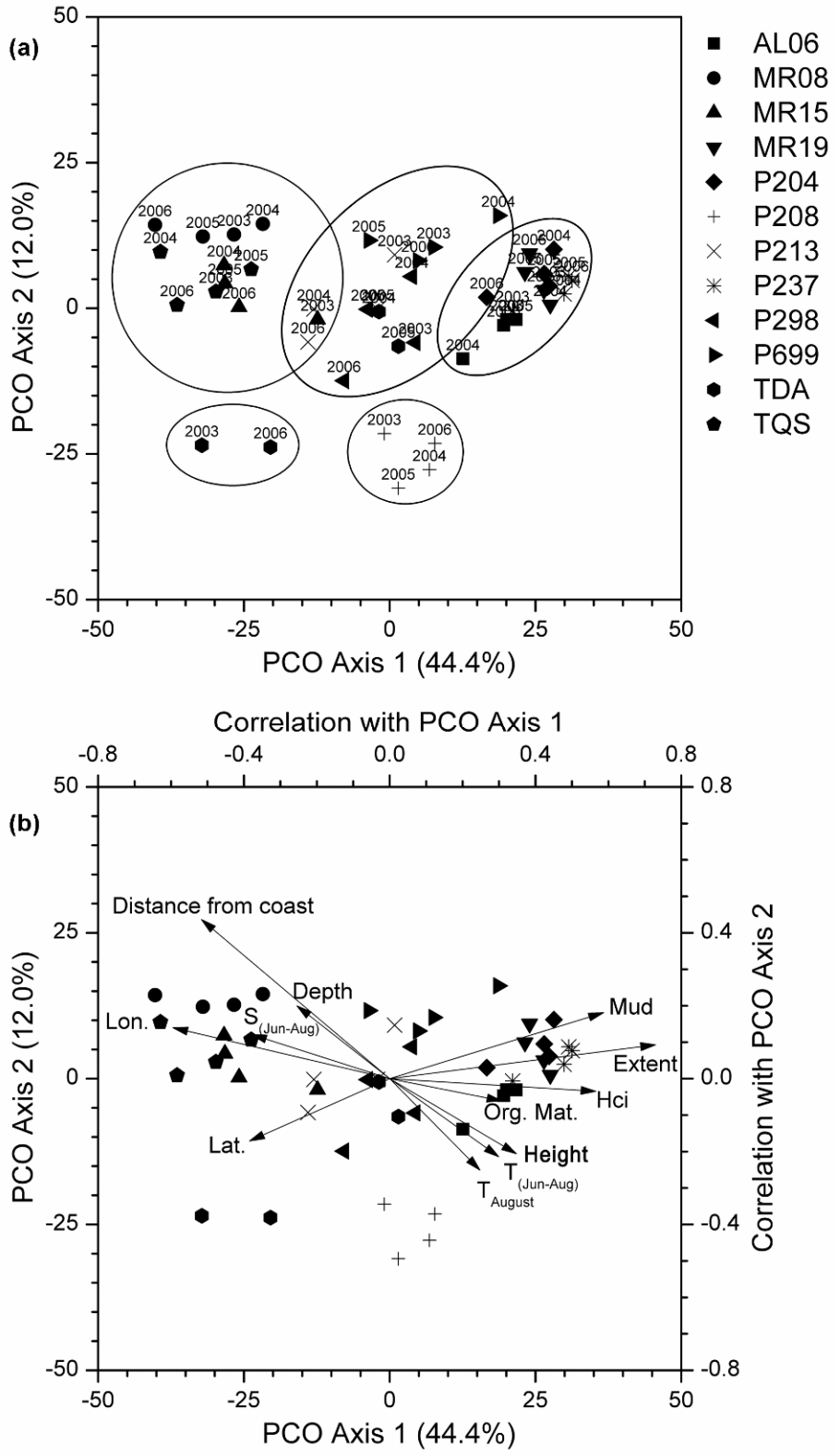


Fig. 3. PCO unconstrained ordination plot (i.e. metric MDS) based on Bray-Curtis dissimilarities of square rout-transformed epibenthic assemblages percent cover data: a) symbols represent sampling sites while year are indicated by numbers, lines show clusters obtained at an arbitrary similarity level of 55%; b) correlation of environmental variable with PCO Axes, represented by superimposed vectors.

Correlation between epibenthic assemblages and environmental variables

Vectors superimposed on the PCO plot graphically represented the relationships between environmental variables and patterns of similarity of the epibenthic assemblages (Fig. 3b). Multivariate multiple regressions indicated that the environmental variables were significantly correlated with patterns of similarity of the benthic assemblages (Table 6). In particular, the cluster of assemblages located near the coast was related to an increase of mud, sediment organic matter, extent and height of relief and summer seawater temperature, while assemblages far from the shore were related to depth and summer salinity.

Abundance of algal turf and the encrusting sponge *Dictyonella incisa*, significantly increased with the extent and height of the outcrops as well as with mud and organic matter content of nearby sediment, while it decreased with the distance from the coast, longitude and salinity (Table 7). On the contrary, *Lithophyllum stictaeforme*, *Lithothamnion minervae*, *Cliona viridis* and *Polycitor adriaticus* were particularly abundant at sites far from the coast, and were negative correlated with mud sediment content and outcrops extent (Table 7). These results are in agreement with the features of the near shore outcrops, which were generally wider, more elevated from the surrounding bottoms, strongly influenced by fluvial inputs, water temperature and salinity.

Species richness and diversity increased with depth and salinity, and decreased with habitat complexity, height of relief, water temperature and organic and mud content in the nearby sediment respectively (Table 7).

Table 7. Correlation matrix displaying r-values among selected taxa, groups of taxa, diversity indices and habitat complexity with environmental variables (*** P < 0.001; ** P < 0.01; * P < 0.05).

	Extent of relief (Log_{10})	Depth	Height of relief	Habitat complexity	Distance from coast	Longitude	Latitude	Mud (%clay+silt)	Org. Matter (%LOI)	Temperature in August	Mean temp. (June-August)	Mean Sal. (June-August)
Lithophyllum stictaeforme	-0.452 **	0.199	-0.366 *	-0.446 ***	0.537 ***	0.359 *	0.150	-0.302 *	-0.146	-0.247	-0.298 *	0.330 *
Lithothamnion minervae	-0.502 ***	0.095	-0.106	-0.257	0.323 *	0.563 ***	0.454 ***	-0.511 ***	-0.243	-0.166	-0.093	0.119
Cliona viridis	-0.389 **	-0.287 *	0.214	-0.041	-0.126	0.331 *	0.722 ***	-0.516 ***	0.122	0.232	0.230	-0.136
Antho (Antho) inconstans	-0.001	0.443 **	-0.314 *	-0.128	0.170	0.089	-0.445 **	0.070	-0.272	-0.415 **	-0.323 *	0.278
Dictyonella incisa	0.729 ***	-0.480 ***	0.466 ***	0.580 ***	-0.634 ***	-0.739 ***	-0.245	0.635 ***	0.385 **	0.564 ***	0.516 ***	-0.483 ***
Tedania anhelans	-0.444 **	0.309 *	-0.316 *	-0.425 **	0.395 **	0.266	0.038	-0.252	-0.511 ***	-0.239	-0.249	0.366 **
Epizoanthus arenaceus	0.011	-0.053	0.042	-0.058	-0.329 *	-0.248	-0.106	-0.098	0.095	0.132	0.135	-0.143
Polycitor adriaticus	-0.513 ***	-0.003	-0.089	-0.302 *	0.298 *	0.461 ***	0.448 ***	-0.422 **	-0.146	0.009	-0.038	0.115
Calcareous algae	-0.513 ***	0.150	-0.308 *	-0.416 **	0.525 ***	0.484 ***	0.311 *	-0.414 **	-0.162	-0.227	-0.236	0.294 *
Algal turf	0.698 ***	-0.258	0.316 *	0.552 ***	-0.374 **	-0.476 ***	-0.296 *	0.551 ***	0.312 *	0.190	0.263	-0.381 **
Boring sponge	-0.075	0.261	-0.365 *	-0.313 *	0.427 **	0.219	-0.010	0.026	-0.224	-0.087	-0.144	0.194
Colonial ascidians	-0.558 ***	0.076	-0.169	-0.389 **	0.373 **	0.488 ***	0.419 **	-0.465 ***	-0.154	-0.052	-0.131	0.161
S	-0.244	0.415 **	-0.429 **	-0.371 **	0.218	0.084	-0.383 **	-0.131	-0.419 **	-0.481 ***	-0.556 ***	0.608 ***
N1	-0.520 ***	0.338 *	-0.350 *	-0.514 ***	0.241	0.270	-0.056	-0.342 *	-0.223	-0.377 **	-0.445 **	0.469 ***
N10	-0.649 ***	0.345 *	-0.329 *	-0.537 ***	0.375 **	0.498 ***	0.225	-0.514 ***	-0.260	-0.204	-0.233	0.154

Discussion

The epibenthic assemblages of coralligenous outcrops were mainly composed, in terms of percent cover, by algal turf, calcareous algae and sponges. Results highlighted the importance and the structural role of macroalgal species (Curiel et al. 2010) that has been largely neglected by previous researches (Casellato et al. 2007; Gabriele et al. 1999). Similarly, sponges' richness has been largely disregarded (5 taxa in Gabriele et al. 1999, 13 in Molin et al. 2003; 27 in Casellato et al. 2007). In the present study, 40 different species of sponges were found, including 8 new records for the Italian coast of the northern Adriatic Sea.

Distribution and abundance of the epibenthic assemblages among the investigated outcrops differed thorough years and sites, with a spatial heterogeneity

being larger than temporal changes. This pattern of variation was confirmed by the distribution of the most abundant taxa (e.g. *Cliona viridis*, *Lithothamnion minervae*, *Polycitor adriaticus*), which varied among sites but were largely consistent in time. These patterns indicated a great temporal persistence of the organisms that characterize the coralligenous communities, as also observed by Garrabou et al. (2002) in north-western Mediterranean coralligenous assemblages. Temporal fluctuations were mostly evident for non-reef forming organisms as algal turf and other non-calcareous algae.

The environmental factors in a heterogeneous system as coralligenous habitat could greatly change at local and geographical scale therefore their influence is little known and hard to quantify (Ballesteros 2006). Irradiance and sedimentation rate on the investigated outcrops can vary with their distance from coast and depth. Moreover, near shore outcrops were generally wider and more elevated from the surrounding bottoms. Morphological features and geographical location of the outcrops affected the spatial distribution of the assemblages, while hydrological conditions that changed over time were less relevant.

The irradiance values on sea bottom in the study area (Franco 1984) were comparable to those recorded in coralligenous concretions developed on horizontal surfaces in other Mediterranean continental shallow coastal waters (i.e. Tossa de Mar; Ballesteros 2006). Light availability in the study area decreased approaching the coast because of the presence of several fluvial inflows that deeply affect turbidity, sediment and nutrients supply and phytoplankton growth. Therefore, distance from the coast and river mouths could be included among the drivers of the spatial variability observed in the northern Adriatic epibenthic assemblages. As a result, algal turf was more abundant in the sites near the coast with high mud and organic matter contents in the surrounding bottoms. On the contrary, the calcareous algae *Lithophyllum stictaeforme*,

Lithothamnion minervae and the erect sponge *Tedania anhelans* were positively correlated with distance from the coast and negatively correlated with mud contents in the surrounding bottoms. These patterns can be explained by the higher resistance to sedimentation and turbidity of algal turf compared to erect and encrusting organisms. Algal turf are known to be able to spread very quickly by vegetative reproduction, independently by the stress regime (Airoldi 1998; Gorgula and Connell 2004; Balata et al. 2005).

Habitat complexity could affect the distribution and abundance of some species, as well as species diversity (Archambault and Bourget 1996 and references therein). Morphologically complex habitat have been shown to be normally associated with a greater species richness (Bergeron and Bourget 1986; Johnson et al. 2003). These observations are in contrast with the present results that showed a negative correlation between habitat complexity and species richness and diversity. The relation between habitat complexity and diversity could be affected by the spatial scale considered here, as habitats could appear homogenous or heterogeneous depending on the spatial scale of observation (Kolasa and Rollo 1991). In the studied area, the most morphologically complex outcrops were located near the shore, where algal turf monopolized space under high sediment deposition, reducing local spatial scale species diversity.

Mediterranean coralligenous habitats showed large spatial and temporal variability at multiple scales. Natural variability of these systems could alter our ability to detect the effect of any natural or anthropogenic disturbance event, and to predict their ecological processes (Denny et al. 2004). In order to protect and manage this marine environment, comprehension of patterns and causes of its variability become a focal point. This regional scale study provides information on the spatial-temporal variability of epibenthic assemblages and on the distribution pattern of the main

organisms. This knowledge could be useful to develop effective growing indicators and ecological status indices for the northern Adriatic coralligenous outcrops based on the ratio between reef builders and bioeroders. The possible effects of some environmental factors have been underlined but further correlative and manipulative studies should be done to investigate the specific role of these factors.

Appendix: Epibenthic sessile flora and fauna reference collection (* new records for the northern Adriatic Sea).

Class	Family		Species
Florideophyceae	Halymeniaceae		*Halymenia floresii* (Clemente y Rubio) C. Agardh, 1817
		*	*Halymenia latifolia* P.L. Crouan & H.M. Crouan ex Kützing, 1866
	Rhodymeniaceae		*Botryocladia botryoides* (Wulfen) Feldmann, 1941
	Peyssonneliaceae		*Peyssonnelia polymorpha* (Zanardini) F. Schmitz, 1879
	Corallinaceae	*	*Lithothamnion minervae* Basso, 1995
			Lithophyllum stictaeforme (Areschoug in J. Agardh) Hauck, 1978
Ulvophyceae	Ulvaceae		*Ulva laetevirens* Areschoug, 1854
Demospongiae	Plakinidae		*Oscarella lobularis* (Schmidt, 1862)
	Geodiidae		*Geodia cydonium* Jamenson, 1811
	Clionaidae		*Cliona celata* Grant,1826
			Cliona rhodensis Rützler & Bromley, 1981
			Cliona viridis Schmidt, 1862
		*	*Cliona thoosina* Topsent, 1887
			Pione vastifica (Hancock, 1849)
	Tethydae		*Tethya aurantium* (Pallas, 1766)
	Polymastiidae		*Polymastia mamillaris* (Müller, 1806)
	Suberitidae	*	*Pseudosuberites sulphureus* (Bean in Bowerbank, 1866)
			Suberites domuncula (Olivi, 1792)
	Chondrillidae		*Chondrosia reniformis* Nardo, 1847
	Microcionidae	*	*Antho* (*Antho*) *inconstans* (Topsent, 1925)
	Coelosphaeridae		*Lissodendroryx* (*Lissodendroryx*) *isodictyalis* (Carter, 1882)
	Microcionidae		*Clathria* (*Clathria*) *compressa* (Schmidt, 1862)
	Hymedesmiidae		*Phorbas tenacior* (Topsent, 1925)
			Phorbas fictitius Bowerbank, 1866
	Tedaniidae		*Tedania* (*Tedania*) *anhelans* Lieberkühn, 1849
	Myxillidae		*Myxilla* (*Myxilla*) *rosacea* (Lieberkühn, 1859)
	Esperiopsidae	*	*Ulosa stuposa* Esper, 1794
	Mycalidae		*Mycale* (*Mycale*) *massa* (Schmidt, 1862)
	Axinellidae		*Axinella damicornis* (Esper, 1794)
			Axinella polypoides Schmidt, 1862
	Bubaridae	*	*Bubaris vermiculata* (Bowerbank, 1866)
	Dictyonellidae		*Acanthella acuta* Schmidt, 1862
		*	*Dictyonella incisa* (Schmidt, 1880)
	Agelasidae		*Agelas oroide*s Schmidt, 1864
	Chalinidae		*Haliclona* (*Haliclona*) *simulans* (Johnston, 1842)
			Haliclona (*Reniera*) *mediterranea* Griessinger, 1971
	Chalinidae	*	*Haliclona* (*Soestella*) cfr. *mamillata* (Griessinger, 1971)
	Petrosidae		*Petrosia* (*Petrosia*) *ficiformis* (Poiret, 1789)
	Ircinidae		*Sarcotragus spinosulus* Schmidt, 1862
			Ircinia variabilis (Pallas, 1766)
	Spongiidae		*Spongia* (*Spongia*) *officinalis* Linné, 1759
	Dysideidae		*Dysidea fragilis* (Montagu, 1818)
			Dysidea avara (Schmidt, 1862)
	Aplysinidae		*Aplysina aerophoba* Nardo, 1843
			Aplysina cavernicola Vacelet, 1959
	Ianthellidae		*Hexadella racovitzai* Topsent, 1896
Hydroidomedusae	Eudendriidae		*Eudendrium* spp. Ehrenberg, 1834
	Tubulariidae		*Ectopleura crocea* (L. Agassiz, 1832)
Anthozoa	Hormathiidae		*Adamsia carciniopados* (Otto, 1823)
	Paralcyoniidae	*	*Paralcyonium spinulosum* (Delle Chiaje, 1822)
		*	*Maasella edwardsi* (De Lacaze-Duthiers, 1888)

	Sagartiidae		*Cereus pedunculatus* (Pennant, 1777)
	Cornulariidae		*Cornularia cornucopiae* (Pallas, 1766)
	Aiptasiidae		*Aiptasia mutabilis* (Gravenhorst, 1831)
	Caryophyllidae		*Caryophyllia smithii* Stockes e Broderip, 1828
	Faviidae		*Cladocora caespitosa* (Linnaeus, 1767)
	Dendrophylliidae		*Leptopsammia pruvot*i Lacaze-Duthiers, 1897
	Epizoathidae		*Epizoanthus* spp. Gray, 1867
	Parazoanthidae		*Parazoanthus axinellae* (Schmidt, 1862)
	Cerianthidae		*Cerianthus membranaceus* (Spallanzani, 1784)
Polychaeta	Sabellidae		*Sabella spallanzanii* (Claparède, 1868)
			Bispira spp. Krøyer, 1856
	Serpulidae		*Serpula vermicularis* Linnaeus, 1767
			Serpula concharum Largerhans 1880
			Pomatoceros triqueter (Linnaeus, 1767)
			Hydroides pseudouncinata pseudouncinata Zibrowius 1971
Polyplacophora	Chitonidae		*Chiton olivaceus* Spengler, 1797
Gastropoda (Prosobranchia)	Vermetidae		*Serpulorbis arenarius* (Linnaeus, 1767)
Bivalvia (Pteromorphia)	Anomiidae		*Anomia ephippium* Linnaeus 1758
	Arcidae		*Arca noae* Linnaeus, 1758
	Mytilidae		*Mytilus galloprovincialis* Lamark, 1819
	Pinnidae		*Pinna nobilis* Linnaeus, 1758
			Atrina pectinata (Linnaeus,1767)
	Ostreidae		*Ostrea edulis* (Linnaeus, 1758)
Bivalvia (Heterodonta)	Gastrochaenidae		*Gastrochaena dubia* (Pennant, 1777)
Gymnolaemata	Phidoloporidae		*Rhynchozoon neapolitanum* Gautier, 1962
Ascidiacea	Pycnoclavellidae	*	*Pycnoclavella* cfr. *taureanensis* Brunetti, 1991
	Polycitoridae		*Cystodytes dellechiajei* (Della Valle, 1877)
			Polycitor adriaticus (Drasche, 1883)
	Polyclinidae		*Aplidium conicum* (Olivi, 1792)
		*	*Aplidium tabarquensis* Ramos-Espla, 1991
		*	*Aplidium* cfr. *densum* (Giard, 1872)
	Ascidiidae		*Phallusia mammillata* (Cuvier, 1815)
			Phallusia fumigata (Grube, 1864)
	Styelidae		*Styela plicata* (Lesueur, 1823)
			Botryllus schlosseri (Pallas, 1776)
	Pyuridae		*Microcosmus vulgaris* Heller, 1877
			Pyura microcosmus (Savigny, 1816)
			Ascidiella aspersa (O.F. Müller, 1776)

Manuscript 2. Short and long-term colonization patterns of coralligenous epibenthic assemblages of the northern Adriatic Sea

Introduction

The composition of epibenthic assemblages can be strongly influenced by the initial settlement and recruitment of individuals (Downes and Keough 1998, Glasby 1998). Local variation in the recruitment processes could be affected by micro-scale habitat heterogeneity (Bourget et al. 1994), biotic interactions (Osman and Whitlatch 1998, Hunt and Scheibling 1997, Smith and Witman 1999; Pawlik et al. 1991), larval supply (Underwood and Fairweather 1989, Bertness et al. 1996) and larval behaviour (Rodriguez et al. 1993). Artificial substrates have been largely used to study spatial and temporal variability of species recruitment (Keough and Downes 1982; Keought, 1983; Turner and Todd 1993; Glasby 1998; Watson and Barnes 2004; Rule and Smith 2005; Denitto et al. 2007) and the effect of biotic and abiotic factors on recruitment processes (Anderson and Underwood 1997; Osman and Whitlatch 2004; Krohling and Zalmon 2008; Cabanellas-Reboredo et al. 2009) even if several studies have revealed that complexity and materials of the substrata can affect the heterogeneity and diversity of assemblages (see Guarnieri et al. 2009).

Spatial distribution and temporal variation of epibenthic assemblages of coralligenous rocky outcrops occurring in the northern Adriatic Sea were investigated by Ponti et al. 2011). These assemblages were mainly composed, in terms of percent cover, by algal turf, calcareous algae and sponges. Spatial heterogeneity, at local and regional scale, prevailed over temporal variation and three main typologies of assemblages can be recognised (Ponti et al. 2011). This variability was related both to the geo-morphological features of the outcrops and to environmental variables but several ecological processes could play a relevant role in structuring the assemblages and

maintain their diversity. In order to assess the role of the short and long terms recruitment processes in determining such variability, patterns of substrate colonization have been investigated in a 3-years field experiment by means of travertine tiles placed in contact with the natural substrates in three different sites. Differences in composition and abundance of species colonising tiles in relation to local and regional spatial scale were quantified in both short-term (first year) and long-term (3-years) analysis. At the end of the experiment, assemblages colonising artificial substrates were compared with those observed in the natural surrounding rocky habitat.

Materials and methods

Study area

Several coralligenous subtidal reefs occur in soft silty-sandy sediments of the northern Adriatic continental shelf offshore Chioggia and Venice between 19 and 27 metres in depth, ranging in size from only a few to several thousands square metres, and up to 4 metres in height from surrounding bottoms (Ponti et al. 2011). According to previous studies, three main typologies of assemblages, in term of species composition and abundance, were detected: i) four outcrops located near the shore (AL06, MR19, P204, P237), dominated by algal turf and encrusting sponges; ii) three small outcrops quite far from the coast (MR08, MR15, TQS), characterised by red calcareous algae and colonial ascidians and iii) three south-eastern outcrops (P213, P298, P699), which showed intermediate abundances of algal turf and encrusting algae (Ponti et al. 2011). One site for each group of these northern Adriatic biogenic reefs was randomly chosen (Fig.1-Tab. 1).

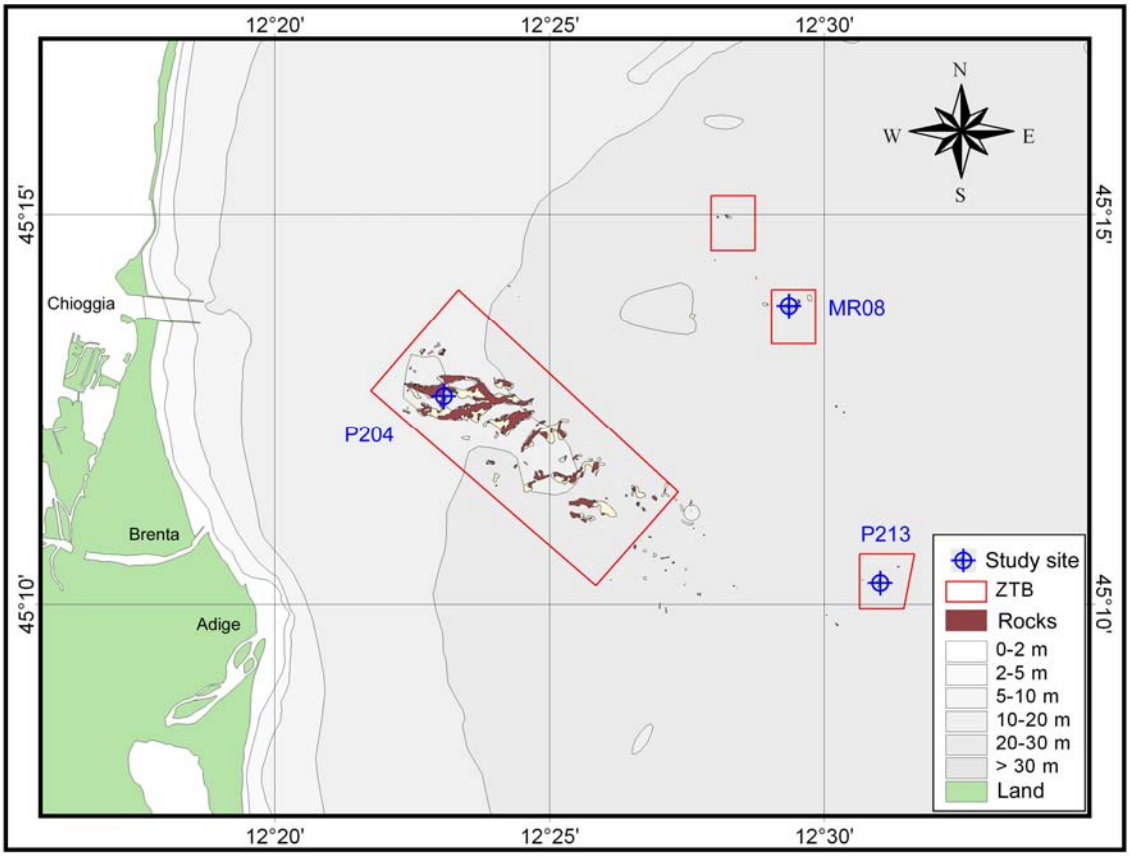


Figure 1. Map of study area, showing the three investigated sites.

Table 1. Location (geographic coordinates, datum wgs84) and geo-morphological features (depth, distance from the coast, extent and height of relief) of the study sites.

Site	Lat N	Lon E	Depth (m)	Coast Dist. (km)	Extent (m^2)	Height (m)
MR08	45° 13.831'	12° 29.354'	22.2	14.6	2,096	1.5
P204	45° 12.674'	12° 23.076'	20.2	6.6	276,297	2.2
P213	45° 10.270'	12° 31.013'	25.4	15.0	1,288	1.2

Experimental set-up and data collection

Overall, 144 tiles were deployed in August 2005 at the three study sites. Three plots, some metres apart, were randomly selected at each site and 16 travertine tiles (15.0 x 11.5 x 1.0 cm) were located in each plot. Travertine is a form of natural limestone deposited by mineral springs, formed by a process of rapid precipitation of calcium carbonate. These features made it chemically similar to the natural carbonate substratum of the outcrops. Each tile was anchored to the horizontal natural hard bottom by means

of steel nails. Tiles were photographically sampled in January, June, August and October 2006, August 2007 and August 2008, which correspond to 5th, 10th, 12th, 14th, 24th, 36th month after the deployment, respectively. Natural assemblages were photographically sampled close to each experimental plot at each site in August 2008. All the photo-samples were collected using an Olympus Cammedia C-7070 WZ underwater digital camera (7 Mpixel) equipped with a TTL strobe and two 50 Watt halogen lights. Photographic samples of natural assemblages were carried out using a frame with dimension of 17.0 x 22.6 cm, 0.0384 m^2. A rigid spacer connected to the camera guaranteed constant distance and parallelism between focal plane and bottom.

Four random photo-samples of the tiles for each plot and sampling date and four random photo-samples of the natural assemblages in August 2008 for each plot, were analysed. Abundance of sessile species colonising tiles were estimated as percent cover, for the bivalves *Anomia ephippium* were also counted the number of specimens per sampled area. Percent cover of sessile organisms was quantified by superimposing a grid of 100 equal sized squares and identifying all taxa visible within each quarter of these squares, corresponding to 0.25% of the total sampled area (Meese and Tomich 1992; Dethier et al. 1993). Percent cover was related to the total readable area of each image, obtained subtracting dark and blurred zone or portion covered by motile organisms. Organisms were identified in accordance with a species reference collection, and assigned to morphological and ecological groups. The endolithic bioeroder bivalve *Gastrochaena dubia* was identified and quantified by counting the siphon holes.

Experimental design and statistical analysis

Three different experimental designs were used to investigate the short-term colonisation patterns (i.e. intra-annual sampling within 14 months from tiles

positioning), the long-term settlement trends (i.e. inter-annual sampling for 3 years) and the differences in assemblages between artificial and natural substrates. Short term colonization patterns were analysed to test for differences among dates (4 random levels: January, June, August and October 2006), sites (3 fixed levels: P204, MR08, P213) and plots (3 levels, random, nested in sites).

Differences in the long-term temporal pattern were analysed among dates (3 random levels: 2006, 2007, 2008), sites (3 fixed levels: P204, MR08, P213) and plots (3 levels, random, nested in sites).

At the end of the experiment, assemblages were compared between substrate type (2 fixed levels: natural and artificial), sites (3 fixed levels: P204, MR08, P213) and plots (3 levels, random, nested in sites).

Epibenthic assemblages were analysed in terms of percent cover of the taxa found. Species diversity, in terms of Shannon index (H', log 2 based) and its corresponding components: species richness (as number of taxa, *S*) and species evenness (as Pielou index, J'), were calculated for each replicate sample.

Distance-based three-way permutational analysis of variance (PERMANOVA; Anderson and ter Braak 2003) was applied to the three experimental designs to test for differences related to the investigated factors. Univariate analyses were based on the Euclidean distances on untransformed data, while multivariate tests were based on Bray-Curtis similarities on squared root transformed data. Similarities among assemblages were graphically represented by ordination plots obtained using the principal coordinate analysis (PCO, i.e. metric multidimensional scaling; Gower 1966). Relationship between the assemblage's similarity patterns and the most abundant species were investigated by multivariate multiple regression using the DISTLM

forward procedure that gives a selection of the species that better explain the observed patterns (McArdle and Anderson 2001; Anderson 2004).

Results

Short-term colonization patterns

The recruited assemblages appeared heterogeneous at local scale and well differentiated among sites since the beginning. Analysing the recruited assemblages patterns in 4 dates within the first 14 months after the tiles deployment, PERMANOVA highlighted the significance of the interaction terms Da x Pl(Si) and Da x Si, indicating that differences between assemblages varied across time at the both spatial scale considered: sites and plots (Table 1). The sampling dates showed four different situations in the temporal succession of the assemblages structuring: i) an early period of high heterogeneity at small spatial scale (on January) ii) a time of high differences between assemblages of different sites (on June; pair-wise test: MR08 $\neq\neq$ P204, MR08 $\neq$ P213, P204 $\neq\neq$ P213) iii) a phase of homogeneity where differences between assemblages couldn't be detected (on August; pair-wise test: MR08 = P204, MR08 = P213, P204 = P213); and iv) a final stage which showed differences among site P204 and the others two sites MR08 and P213 (on October; pair-wise test: MR08 $\neq\neq$ P204, P213 $\neq\neq$ P204). The temporal trends of the assemblages of the sites MR08 and P213 were very similar in term of direction even if the main differentiation occurred among June and August in P213 and among January and June in MR08. The site P204 displayed a lower general temporal variation in the opposite direction in comparison with the other sites (Fig. 2a).

Table 1. Results from PERMANOVA on Bray-Curtis similarities of square rout-transformed epibenthic percent cover data in the short-term analysis.

Source	df	SS	MS	Pseudo-F	P(perm)	Unique perms
SI	2	23,693	11847.0	3.8881	0.0021	9,932
DA	3	18,838	6279.2	7.1891	0.0001	9,938
PL(SI)	6	9,338	1556.4	1.7819	0.0518	9,928
DAxSI	6	11,691	1948.5	2.2309	0.0215	9,931
DAxPL(SI)	15	13,101	873.4	2.9306	0.0001	9,856
Res	99	29,505	298.0			
Total	131	111,310				

The relationships between single species and patterns of similarities of the epibenthic assemblages were graphically represented by correlation vectors superimposed on the PCO plot (Fig. 2b). Multivariate multiple regressions (DISTLM) indicated that non colonised substrate, algal turf, serpulids, *Lithothamnion minervae*, *Tedania anhelans*, *Anomia ephippium*, *Lithophyllum sticteformae*, sediment and *Policitor adriaticus* showed a significant correlation with patterns of similarity of the benthic assemblages (explained proportion of the assemblages variability according to the DISTLM forward procedure: 40.87%, 15.91%, 15.38%, 9.05%, 4.27%, 4.03%, 3.80%, 1.58%, 1.39% respectively) (Table 2). Patterns of similarity of MR08 and P213 assemblages in the first and second sampling dates were mainly explained by the non-colonised substrate, the bivalve *Anomia ephippium* and serpulid polychaetes while in the second and last sampling date by calcareous algae *Lithothamnion minervae* and *Lithophyllum stictaeforme* and the sponge *Tedania anhelans*. The temporal and spatial differentiations of the P204 assemblages were mainly explained by sediment and algal turf (Fig. 2b).

Table 2. Multivariate multiple regression (DISTLM forward procedure) between epibenthic assemblages similarity pattern and most abundant species.

Variable	SS(trace)	Pseudo-F	P	Prop.	Cumul.
Non colonised substrate	45,500	89.878	0.0001	0.409	0.4088
Algal turf	17,719	47.529	0.0001	0.159	0.5679
Serpulid polychaetes	17,127	70.799	0.0001	0.154	0.7218
Lithothamnion minervae	10,074	61.242	0.0001	0.091	0.8123
Tedania anhelans	4,756	37.139	0.0001	0.043	0.8550
Anomia ephippium	4,486	48.138	0.0001	0.040	0.8953
Lithophyllum stictaeforme	4,236	70.860	0.0001	0.038	0.9334
Sediment	1,759	38.283	0.0001	0.016	0.9492
Sabellaria sand tubes	400	61.808	0.0299	0.004	0.9932

At the first sampling date, 5 month after the beginning of the experiment, travertine tiles were mainly colonised by pioneer species like the bivalves *Anomia ephippium*m and the serpulid polychaetes. The analysis of single taxa showed that the first colonisers varied across plots and sites, in particular, in the early recruitment phase the most abundant species was *Anomia ephippium* (PERMANOVA: Da x Pl(Si) $p<0.01$) in P213 and serpulid polychaetes (PERMANOVA: Si x Da $p<0.01$) in MR08 (Fig 3a-b).

The following recruits were red calcareous algae *Lithothamnion minervae* (PERMANOVA: Da x Pl(Si) $p<0.01$ and Si x Da $0.05<p<0.01$) and *Lithophyllum stictaeforme* (PERMANOVA: Da x Pl(Si) $p<0.01$) in MR08, the sponge *Tedania anhelans* (PERMANOVA: Si x Da and Pl(Si) $p<0.01$) in P213 and algal turf (PERMANOVA: Da x Pl(Si) and Si $p<0.01$) in P204 (Fig. 3 c-d-e-f).

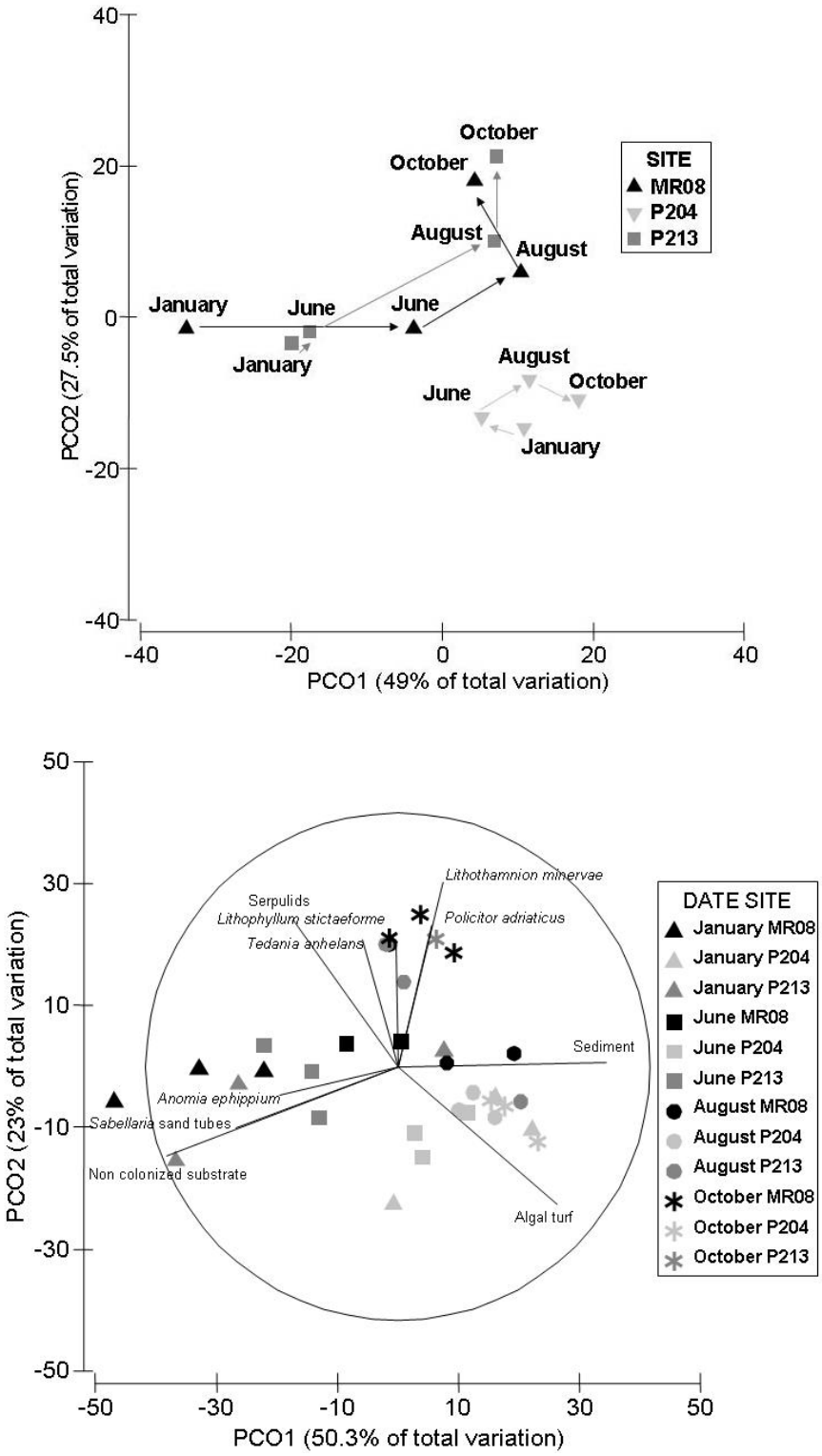


Figure 2. PCO unconstrained ordination (i.e. metric MDS) based on Bray-Curtis similarities of square rout-transformed percent cover data: a) symbols represented sampling dates while colors indicated sites, each point represented the centroid of the observed similarity among the interaction DA x SI; b) each point were the centroid of the observed similarity among replicates and the superimposed vectors represented correlation of single taxa with PCO Axes.

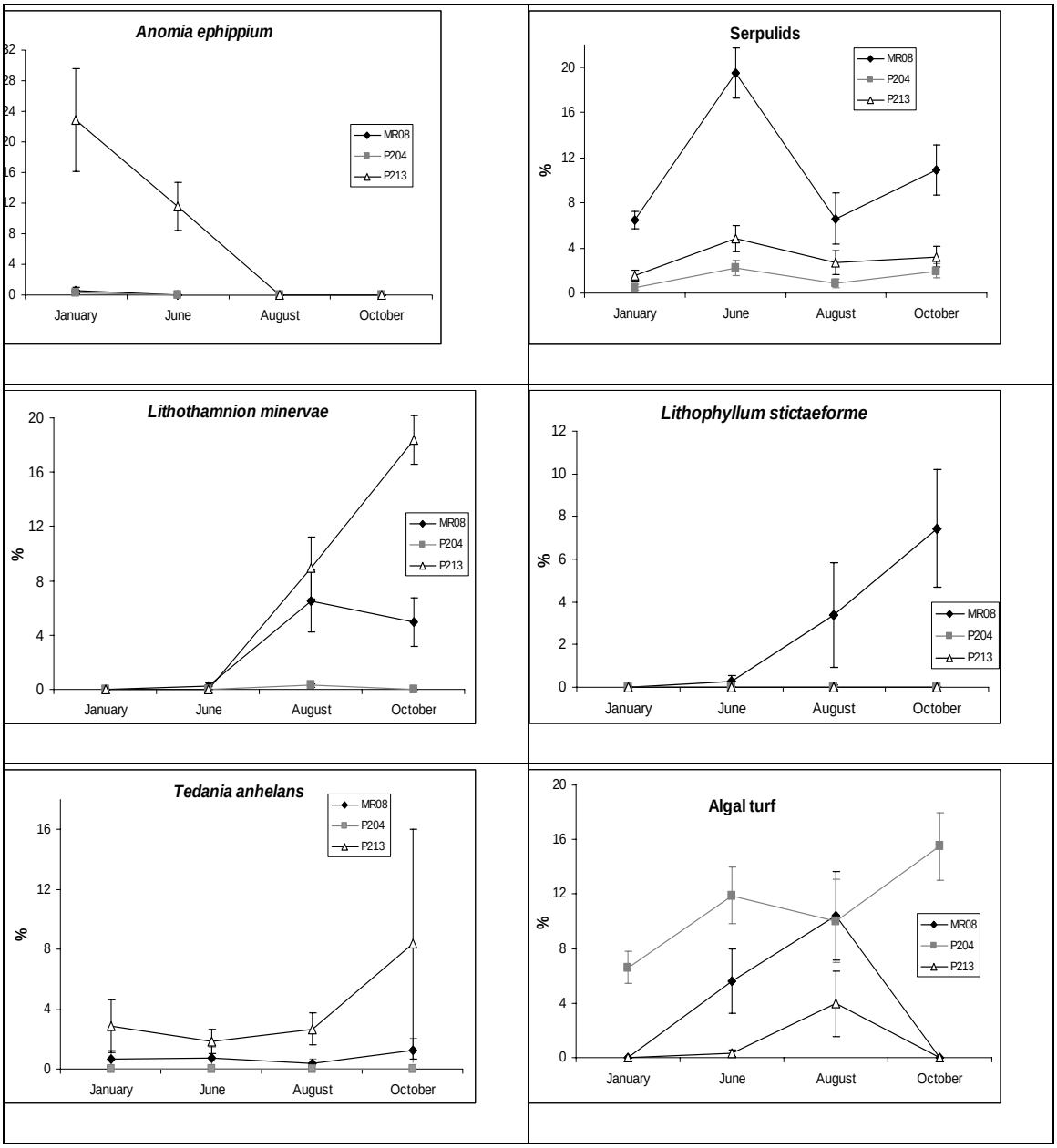


Figure 3. Spatial and temporal trends of the selected species: a) *Anomia ephippium*, b) serpulid polychaetes, c) *Lithothamnion minervae*, d) *Lithophyllum stictaeforme*, e) *Tedania anhelans* f) algal turf (mean values ± SE).

Site-specific significant differences in term of species richness (S) (PERMANOVA: Da and Si $p<0.01$), evenness (J') (PERMANOVA: Da x Pl(Si) $p<0.01$ and Si $p<0.05$) and heterogeneity (H') (PERMANOVA: Da x Pl(Si) $p<0.01$ and Si $p<0.01$) among the pairs of site MR08 - P204 and P204 - P213 were detected. On overall MR08 and P213 showed higher value for all the diversity indices compared to P204 (Fig. 4).

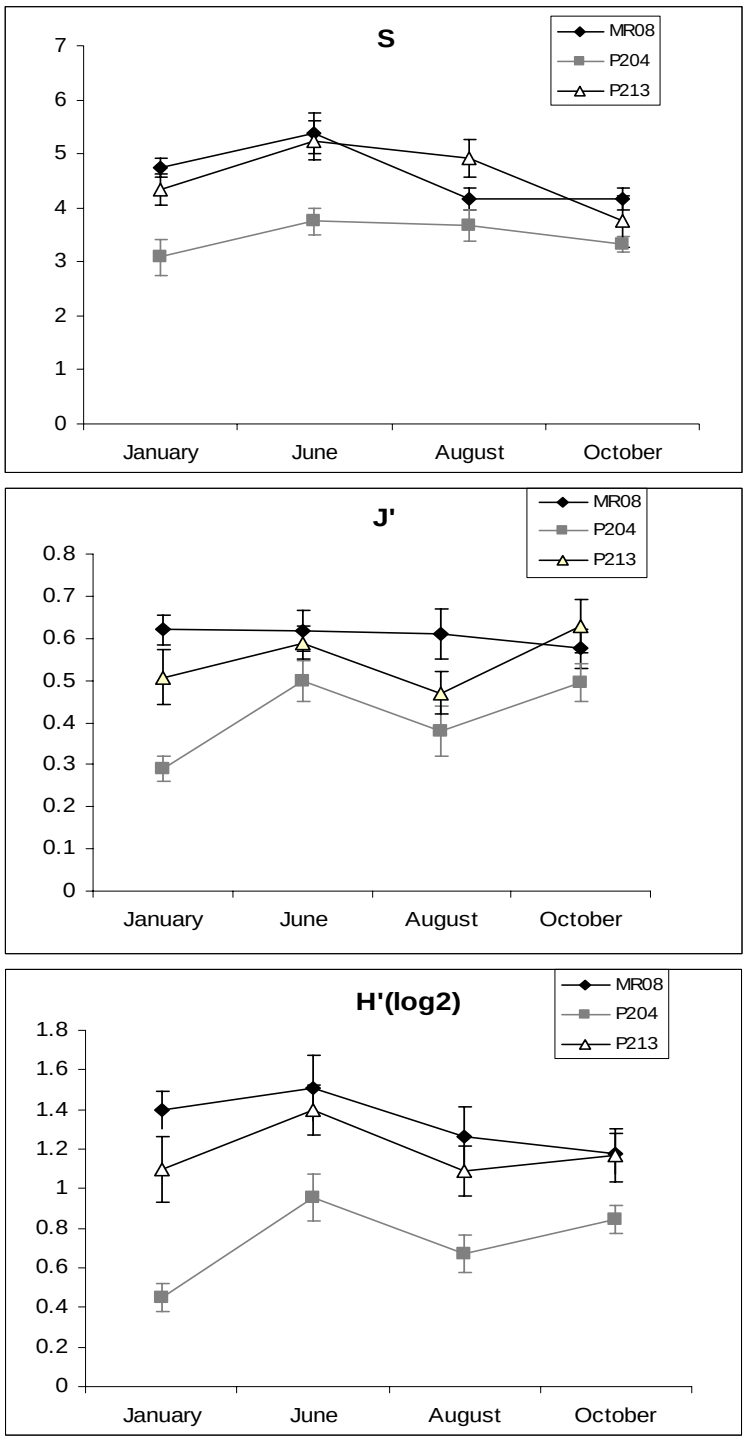


Fig. 4. Spatial and temporal trends of the diversity indices: a) species richness (S), b) species evenness (J') and b) species diversity (H') (mean values ± SE).

Long-term settlement trends

The analysis of the colonising assemblages in August of the three years after the tiles deployment, showed differences through years at both sites and plots spatial scales. The pair-wise test for the interactions Da X Si highlighted a progressive site-specific

temporal differentiation of the assemblages (Table 3). Each site showed a divergent annual trend of the assemblages except for the P213 site whose assemblages in August 2008 seemed to be similar to those recorded in 2006. The taxa that better explained the differences among assemblages were *Lithothamnion minervae*, *Lithophyllum stictaeforme* and serpulid polychaetes in MR08, algal turf in P204 and *Tedania anhelans*, serpulid polychaetes and *Gastrochaena dubia* in P213 (Fig. 5).

Table 3. PERMANOVA results based on Bray-Curtis similarities of square rout-transformed epibenthic percent cover data in the long-term analysis.

Source	df	SS	MS	Pseudo-F	P(perm)	Unique perms
DA	2	10,029	5,014.5	4.531	0.003	9,949
SI	2	31,057	15,529.0	2.962	0.012	9,933
PL(SI)	6	21,921	3,653.5	3.301	0.001	9,910
DAxSI	4	9,881	2,470.3	2.232	0.016	9,932
DAxPL(SI)	10	11,068	1,106.8	2.049	0.000	9,839
Res	75	40,510	540.1			
Total	99	127,190				

The percent cover of algal turf varied thought years among sites (PERMANOVA: Da x Si $p<0.01$ and Pl(Si) $p<0.01$) in particular in the first year it occurred in all sites with a comparable density while in 2007 and 2008 it mainly characterised the site P204 and strongly decreased in MR08 and P213 (Fig. 6a). The calcareous algae *L. minervae* (PERMANOVA: Da x Pl(Si) $p<0.01$) and *L. stictaeforme* (PERMANOVA: Da x Si $p<0.01$) showed a low density in the early period of colonization while they increased with time especially in the site MR08 (Fig. 6b-c). The first colonisers like serpulid polychaetes (PERMANOVA: Da x Pl(Si) $p<0.01$) were particularly abundant in the first year then they fell down with time but always displayed a high variability at small spatial scale (Fig.6-d). The species richness (S) and species diversity (H') significantly increased across years (PERMAVOVA, Da $p<0.01$).

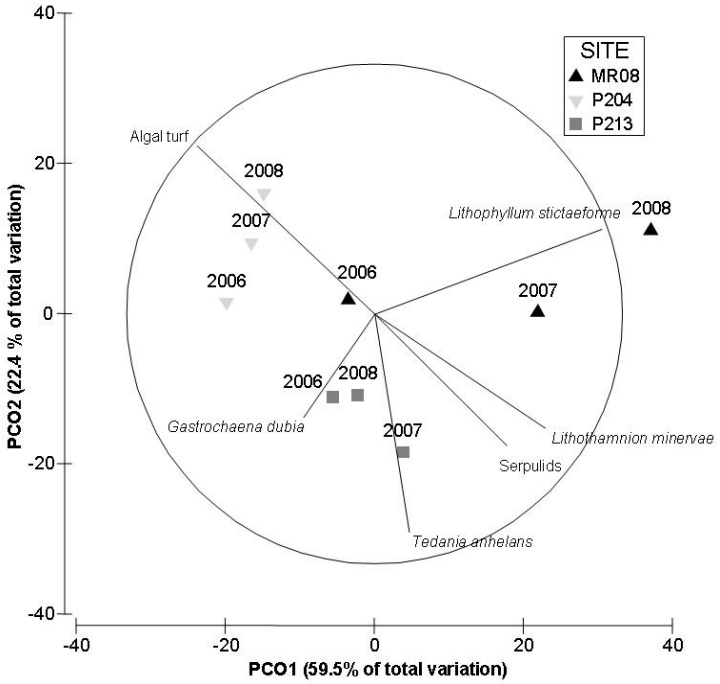


Figure 5. PCO unconstrained ordination (i.e. metric MDS) based on Bray-Curtis similarities of square rout-transformed tile assemblages percent cover data. Each point represented the centroid of the observed similarity among the interaction DA x SI and the superimposed vectors represented correlation of single taxa with PCO Axes.

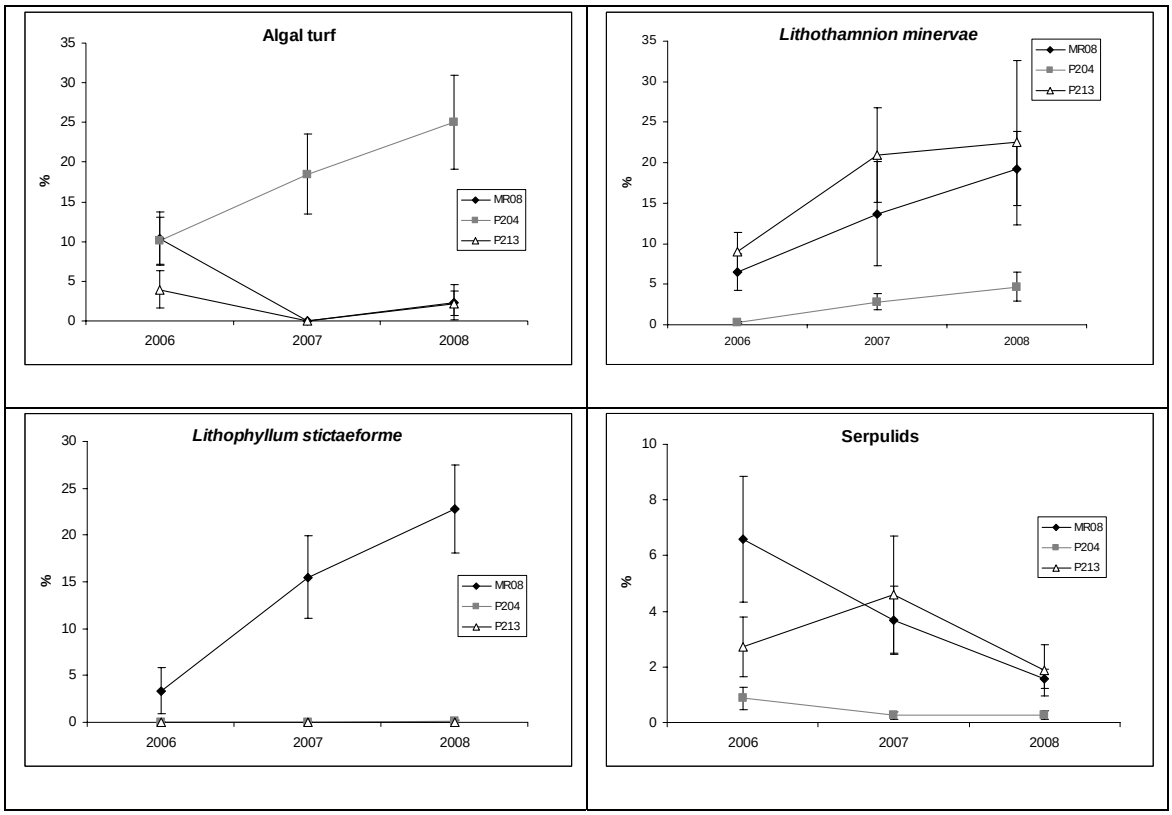


Figure 6. Spatial and temporal trends of the selected species: a) Algal turf b) *Lithothamnion minervae*, c) *Lithophyllum stictaeforme*, d) serpulid polychaetes (mean values ± SE).

Natural vs artificial substrate assemblages

At the end of the experiment (August 2008), assemblages found on the artificial substrate were not different from those naturally present in their respective plots and sites, as confirmed by the PERMANOVA analysis that detected no differences in the interactions Su x Pl(Si) ($p>0.01$) and Su x Si ($p>0.01$). The PCO plot displayed a partial overlapping of the assemblages of natural and artificial substrate of each site highlighting some degree of similarity (Fig. 7). Some of the most abundant species as algal turf, *L. stictaeforme*, *L. minervae*, *Gastrochaena dubia* and serpulid polychaetes varied among plots in relation to different substrate type (PERMANOVA: Su x Pl(Si) $p<0.01$) but the pair-wise test highlighted that differences had to be mainly ascribed to the high heterogeneity at small spatial scale within natural and artificial substrate. Species diversity and evenness did not differ between natural and artificial substrate within each plot and site.

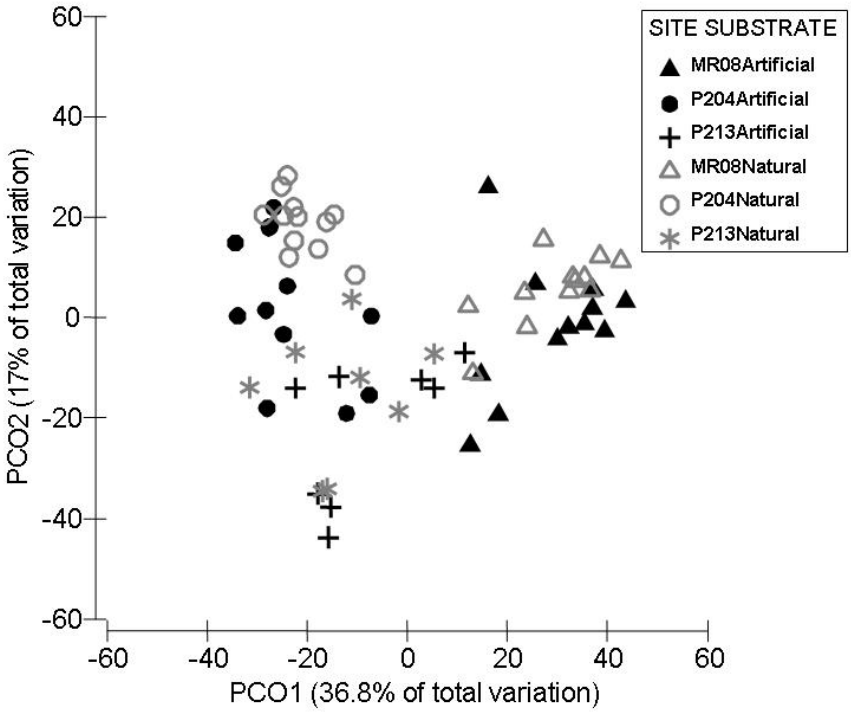


Figure 7. PCO unconstrained ordination (i.e. metric MDS) based on Bray-Curtis similarities of square rout-transformed tile and natural assemblages percent cover data.

Discussion

The recruitment of sessile assemblages on artificial substrates, within the investigated subtidal coralligenous habitat, varied at local and regional spatial scale in both short and long-term analysis. The short-term temporal trend showed an early stage characterised by high heterogeneity of the assemblages, which could be related to the site-specific variability of the first colonisers, this in turn may be due to different larval supply. On August 2006 a phase of relative homogeneity among assemblages occurred, probably due to the seasonal algal bloom that could mask the underlying assemblages variability. An increasing site-specific temporal differentiation of tile assemblages had been observed in the analysis of the long-term recruitment trend jointly with a progressive similarity to the surrounding natural assemblages, especially in regards to the most abundant species. Summarising, the assemblages established on tiles differed among sites from the early stage of colonisation with an increasing diversification trough time. These results supported the important role of the early recruitment in the development and final structure of assemblages.

Several researches highlighted the importance of natural surrounding habitat in determining the composition of assemblages colonising artificial substrate (Myers and Southgate 1980, Edgard 1991, Chapman 2002, Norderhaug et al. 2002). The structure of adjacent habitats appeared to have an important influence on tiles assemblages that reflected the high heterogeneity of the natural communities at the small spatial scale here considered. The geographical position and environmental variables of each site could play an important role in the differences between assemblages structure at regional scale. The increased proportion of algal turf in the tile assemblages of P204 was probably related to the high turbidity and sedimentation rate of this site, located

near the coast where several fluvial inputs occurred. Instead, the high density of calcareous algae in the composition of tile assemblages of MR08, located far from the coast, was probably due the higher level of irradiance (Ponti et al. 2011). Light is considered one of the most important factors affecting the growth and development of coralligenous habitat (Martì et al. 2004). Assemblages colonising tiles after three years from their positioning appeared comparable with natural assemblages in term of most abundant species and species diversity. Moreover, differences among natural assemblages in the three studied sites were maintained on artificial substrates. These results highlighted the usefulness of travertine tiles in the study of coralligenous assemblages development and structuring.

Manuscript 3. Bioconstruction-erosion processes and biomass in the northern Adriatic coralligenous reefs

Introduction

Shallow-water temperate ecosystems have proved to be important contributors to the global inorganic carbon cycle (Mackenzie et al. 2004; Muller-Karger et al. 2005), in particular benthic communities have high primary production and carbonate deposition rate (Milliman and Droxler 1996). These processes could be particularly considerable in the Mediterranean coralligenous habitat characterised by a high abundance of calcareous organisms, which, at the end of their life cycle, contributed to sediments and limestone production by diagenesis and lithification (Ballesteros 2006). Unfortunately, information on calcium carbonate production, export and accumulation on temperate continental shelves are poorly documented (Cebrian et al. 2000).

Bioerosion is another important regulating factor and inherent process in calcium carbonate dominated environments (e.g., Hutchings 1986). It consists in breakdown of the hard substrate by boring organisms (Bromley et al. 1990), mainly macroborer species like sponges, bivalves and polychaetes (Cerrano et al. 2001, Schiaparelli et al. 2005). On overall, bioerosion, in the coralligenous communities, is less studied than the calcification processes, due to the inherent difficulties (Holmes et al. 2009).

In the study of dynamics for the whole coralligenous habitat, benthic community biomass and productivity are essential especially because they can affect the energy flow and organic matter cycling in aquatic ecosystems (Brey 1990, Palmerini and Bianchi 1994).

This study aimed to increase the knowledge on the potential biogenic carbonate production and the erosion processes occurring in the northern Adriatic coralligenous

reefs. Biomass and energetic content of assemblages in these coralligenous habitats were also investigated.

Materials and Methods

This study focused on coralligenous subtidal reefs of the northern Adriatic Sea offshore of Chioggia, where three main types of epibenthic assemblages were previously detected (Ponti et al. 2011). One site for each type of assemblage was randomly selected to perform a long field colonisation experiment. Site P204 belongs to the outcrops dominated by algal turf and encrusting sponges, MR08 is member of the outcrops characterised by red calcareous algae and colonial ascidians, and P213 is among those showing intermediate abundances of algal turf and encrusting algae (Fig. 1 - Tab. 1). On August 2005 forty-eight travertine tiles (15.0 x 11.5 x 1.0 cm) were deployed on the sea bottom of each of the three study sites and arranged within each site in three randomly selected plots some meters apart. Each tile was labelled and weighted before the placement. On August 2008, after three years from their deployment, four tiles for each plot and site were taken to the surface in individual plastic zip-bags and then preserved in a buffered solution of formaldehyde (4%). Unfortunately, one entire plot at P213 site was lost, probably destroyed by trawling. For each tile, percent cover of sessile fauna, abundance of vagile species, biomass and energetic content of epibionts and bioconstruction-erosion processes were measured.

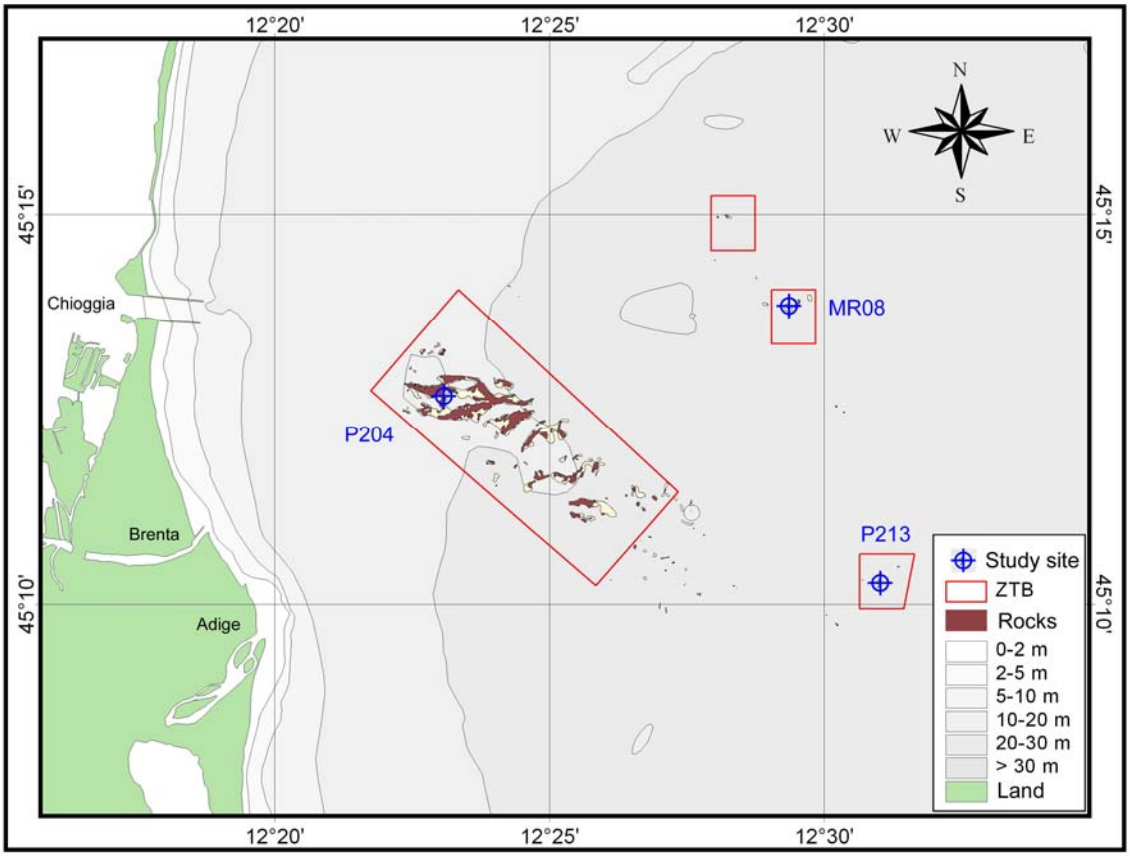


Figure 1. Map of study area, showing the three investigated sites.

Table 1. Location (geographic coordinates, datum wgs84) and geo-morphological features (depth, distance from the coast, extent and height of relief) of the study sites.

Site	Lat N	Lon E	Depth (m)	Coast Dist. (km)	Extent (m^2)	Height (m)
MR08	45° 13.831'	12° 29.354'	22.2	14.6	2,096	1.5
P204	45° 12.674'	12° 23.076'	20.2	6.6	276,297	2.2
P213	45° 10.270'	12° 31.013'	25.4	15.0	1,288	1.2

Vagile and sessile fauna

Vagile species of each tile were identified and counted. Abundance of sessile species colonising tiles were estimated as percent cover by photographing tiles and superimposing a grid of 100 equal sized squares. All the visible taxa within each quarter of these squares, i.e. ± 0.25%, were identified (Meese and Tomich 1992; Dethier et al. 1993). In addition, the number of individuals per tile of small and high density species (i.e. *Pomatocerus triqueter*, *Serpula cuncharum*, *Gastrocaena dubia*, ecc.) were

counted. The abundance of sessile species were estimated separately for either upper and lower tile surface. Both, vagile and sessile species were identified to the lowest possible taxonomic level.

Bioconstruction-erosion processes

All sessile species colonising tiles were scraped out from both upper and lower tile faces. The net balance of inner bioconstruction-erosion processes by endobionts were estimated comparing the original mass of each tile with its mass after removal of external concretion, drying at 80°C for 24 h and then ignition of the organic matter of endobionts still present inside the crevices at 450 °C for 8 h (Luczak et al. 1997). The same protocol was applied to measure the dry-mass (DM), ash-mass (AM) and ash free dry mass (AFDM) of vagile and sessile epibionts pooled in taxonomic groups. Total net bioconstruction-erosion balance were estimated combining the endobionts and epibionts data.

The energetic contents of the epibenthic assemblages, in terms of Joule m^{-2}, were estimated starting from biomass values and by the conversion factors (J/g AFDM) provided by Brey et al. (2001) for most of the main taxonomic groups.

Data analysis

Differences in vagile and sessile species abundances, biomasses and energetic content, as well as, bioconstruction-erosion balance were analysed among sites (Si: 3 levels, fixed: P204, MR08, P213) and plots (Pl: 3 levels, random, nested in sites).

Distance-based two-way permutational analysis of variance (PERMANOVA; Anderson and ter Braak 2003) was applied to test for differences related to the investigated factors. Univariate analyses were based on the Euclidean distances of untransformed

data, while multivariate tests were based on Bray-Curtis similarities of squared root transformed data. Similarities among assemblages were graphically represented by ordination plots obtained using the principal coordinate analysis (PCO, i.e. metric multidimensional scaling; Gower 1966). A selection of the species that better explained the assemblage's similarity patterns were obtained by multivariate multiple regression using the DISTLM forward procedure (McArdle and Anderson 2001).

Percent cover – biomass (g_{AFDM} m^{-2}) conversion factors of the most abundant sessile specie were estimated by linear regression. The probability that the fitting line slope differed from zero was investigated by ANOVA.

Results

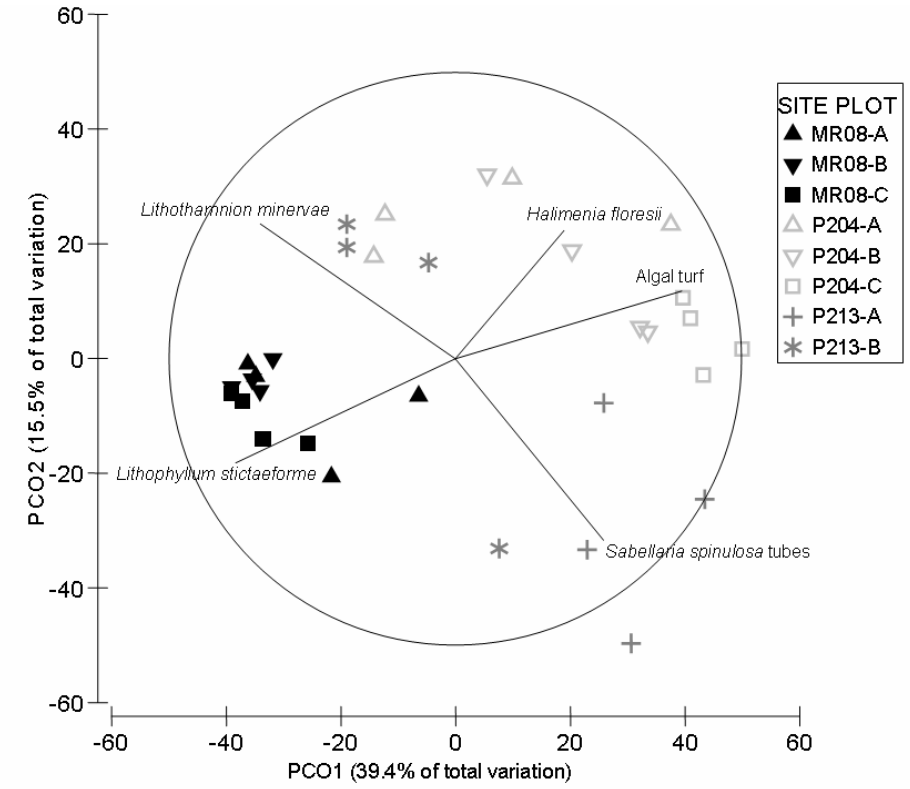
Vagile and sessile flora and fauna

Percent cover of sessile organisms colonising the tile upper-face (Fig. 2-a), significantly differed among plots and sites (PERMANOVA: Pl(Si) $P < 0.01$; Si $P < 0.05$; pair-wise: MR08 ≠ ≠ P204 and MR08 ≠ P213) while those colonising the tile lower-face (Fig. 2-b) varied only among sites, showing a higher site-specific heterogeneity (PERMANOVA: Si $P < 0.001$; pair-wise: MR08 ≠ ≠ ≠ P204, MR08 ≠ P213, P204 ≠ P213). The calcareous algae *Lithophyllum stictaeforme* and *Lithothamnion minervae*, the *Sabellaria spinulosa.* tubes, algal turf and the red algae *Halimeda floresii* mainly characterized the upper-face assemblages while two different species of bryozoans, a not identified encrusting sponge, *Hyalopomatus* sp. tubes and other serpulid polychaetes mainly explained the differences among the lower-face assemblages. Sessile species in term of numbers of individuals for tile differed among plots in the upper-face (PERMANOVA: Pl(Si) $P < 0.01$) and among plots and sites in the lower-face (PERMANOVA: Pl(Si) $P < 0.01$, Si $P < 0.05$). Species that mainly contributed to the observed patterns were

Sabellaria spinulosa., *Gastrocaena dubia* and *Pomatocerus triqueter* tubes in the upper assemblages and *Verruca spengleri*, *Gastrocaena dubia* and *Serpula* spp. tubes in the lower-face.

Overall, 100 vagile taxa were found. The most abundant organisms were Tanaidacea (12%), Cirratuidae (11%), *Dodecaceria concharum* (6%), Syllidae (6%), Copepoda (6%), *Bittium reticulatum* (4%), *Leptochelia savignyi* (4%).

Although most of the single taxa didn't show a clear distribution pattern, vagile assemblages structure significantly differed among plots and sites (PERMANOVA: Pl (Si) $P < 0.001$, Si $P < 0.01$) (Fig. 3).



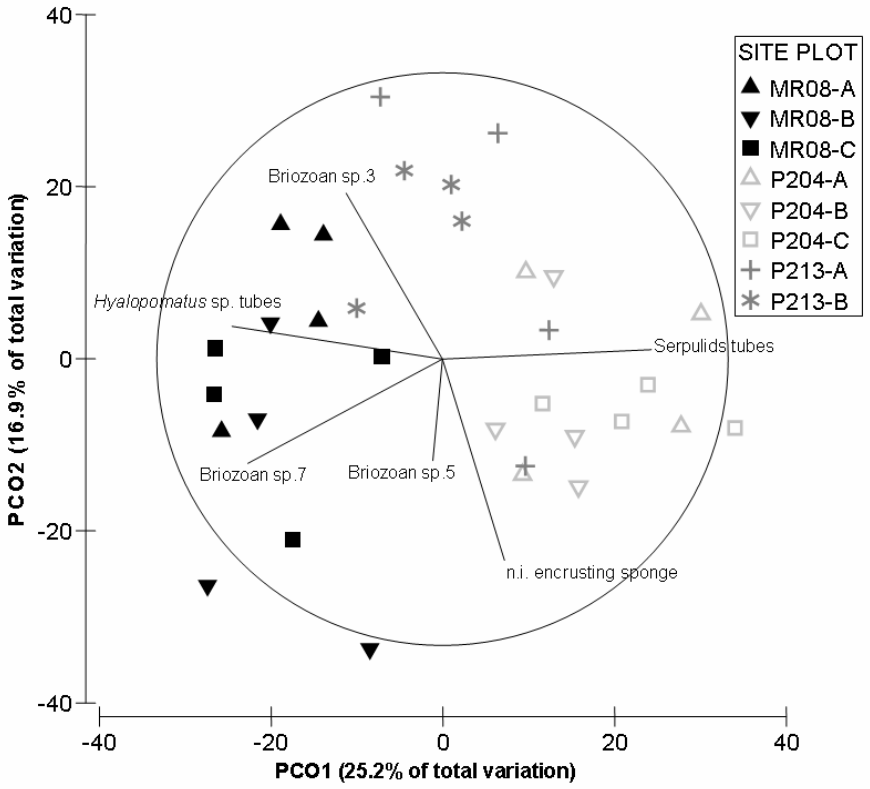


Figure 2. PCO unconstrained ordination plot (i.e. metric MDS) based on Bray-Curtis similarities of square rout-transformed percent cover data, the superimposed vectors represented correlation of single taxa with PCO Axes: a) percent cover of sessile organisms colonising the upper face b) percent cover of sessile organisms colonising the lower face.

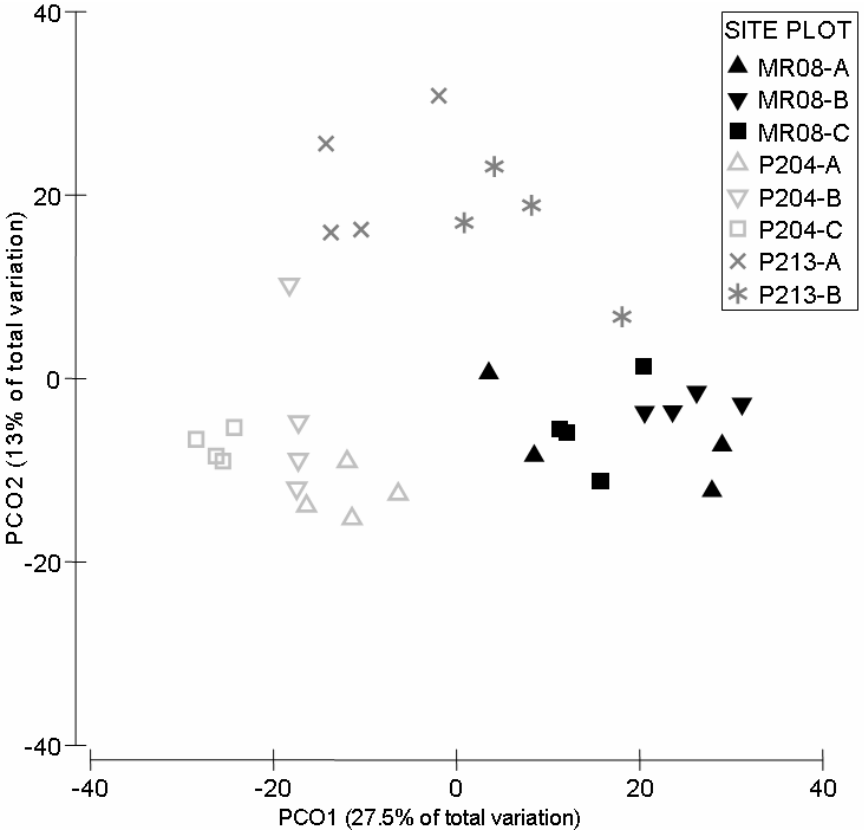


Figure 3. PCO unconstrained ordination (i.e. metric MDS) based on Bray-Curtis similarities of square rout-transformed vagile species data.

Correlation analyses between the abundance of vagile species and the similarity pattern of sessile assemblages on the upper face showed that the gastropod *Bittium reticulatum* and Ostracoda were associated with the P204 assemblages dominated by algal turf and hydroids. The Polyplacophora *Chiton* sp. was more abundant at MR08, dominated by red calcareous algae. Amphipoda sp. 1 and Paguridae density increased in the P213 assemblages, characterised by an intermediate abundance of calcareous algae, algal turf and hydroids (Fig. 4).

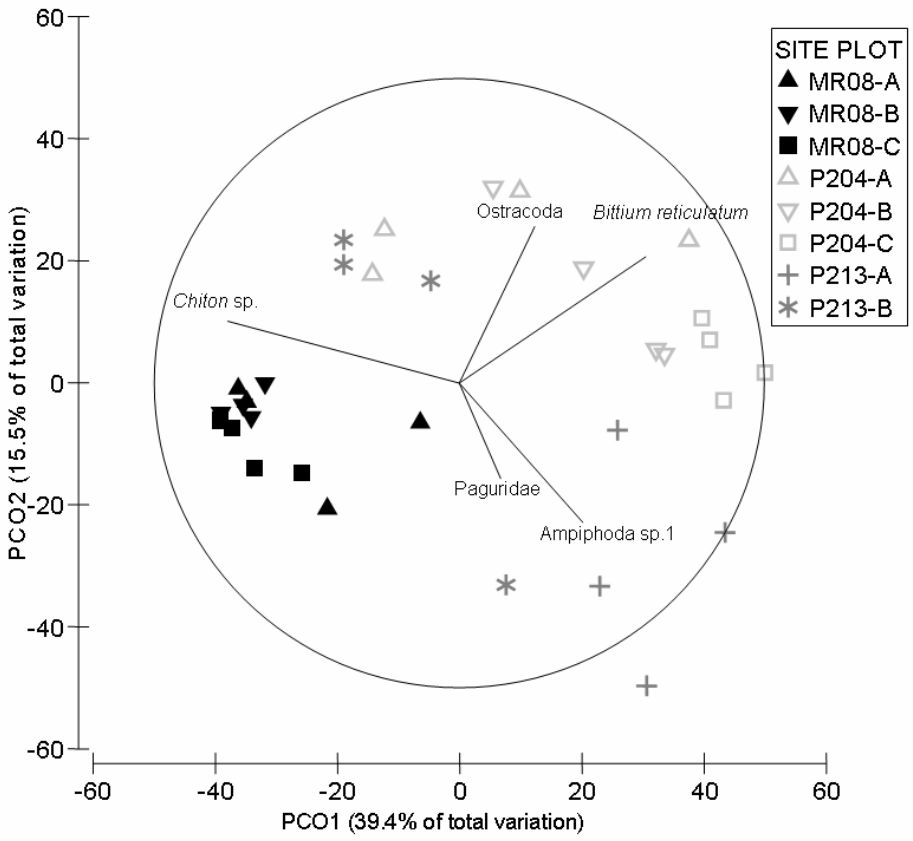


Figure 4. PCO unconstrained ordination (i.e. metric MDS) based on Bray-Curtis similarities of square rout-transformed sessile species cover data (upper face), the superimposed vectors represented correlation of single vagile taxa with PCO Axes.

The abundance of *Bittium reticulatum* was positively correlated with the percent cover of algal turf while the abundance of the grazer *Chiton* sp. decreased with the percent cover of algal turf and increased with the percent cover of calcareous algae (Fig. 5).

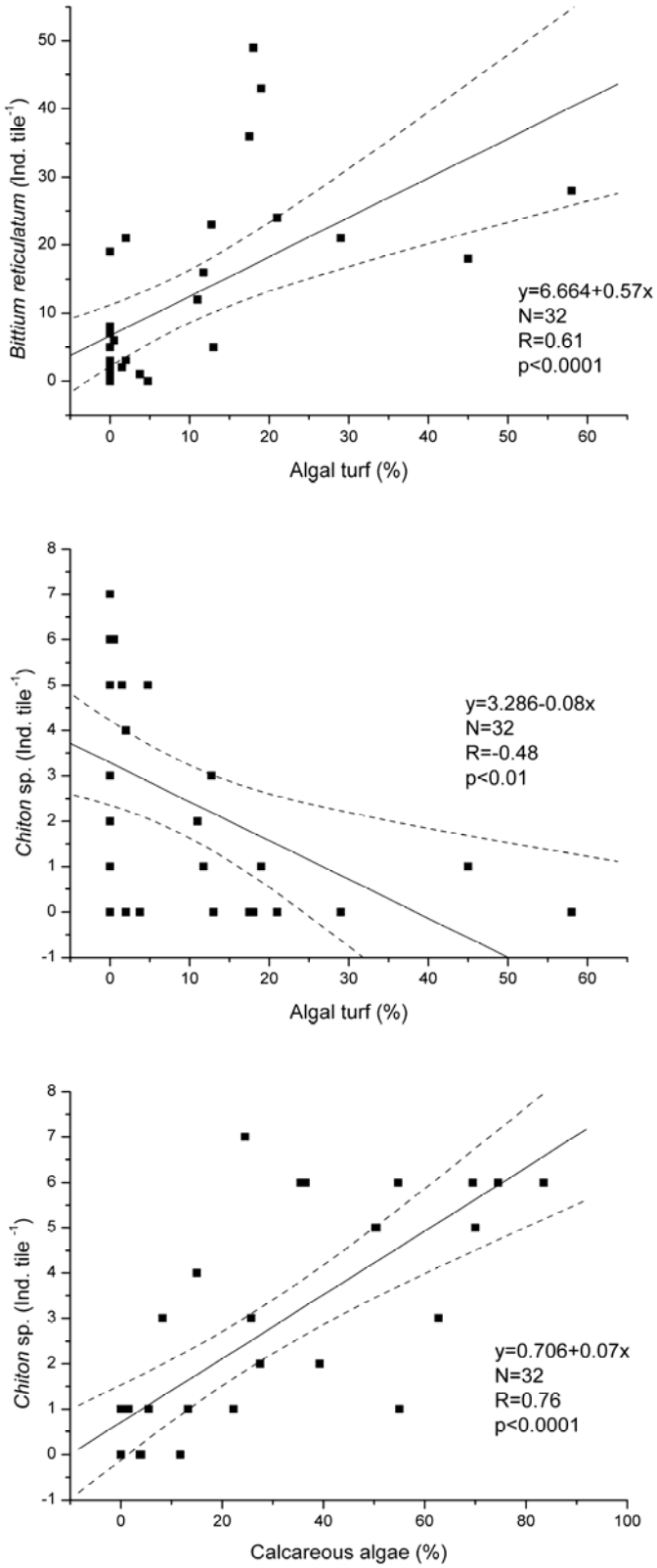


Figure 5. Percent cover of algal turf and calcareous algae *vs.* abundance of the vagile species *Bittium reticulatum* and *Chiton* sp.

Bioconstruction-erosion processes

Inner bioconstruction-erosion net balance by endolithic organisms was slightly negative or almost zero at all sites (Fig. 6) and didn't significantly differ among plots and sites (PERMANOVA: Pl(Si) $P > 0.01$, Si $P > 0.01$).

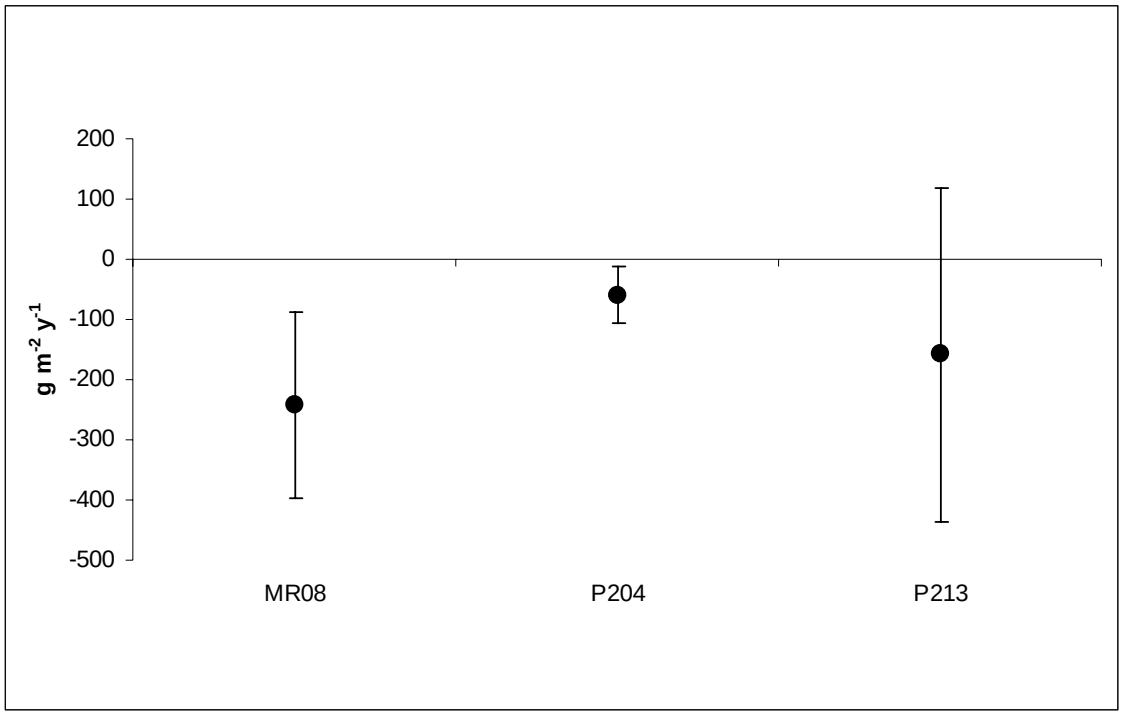


Figure 6. Biocostruction-erosion net balance by endobionts (mean value ± $CL_{95\%}$)

The mean total inorganic mass production by epibionts was 365 (±2.07) g_{AM} m^{-2} y^{-1} and their contribution to carbonate substratum accretion varied only among plots (PERMANOVA: Pl(Si) $P < 0.001$). The major contribution, in all the study sites, derived from serpulid polychaetes with a percentage of 29.5%, 50.42% and 25% in MR08, P204 and P213 respectively. Others important site-specific inorganic mass producers were: calcareous algae and bryozoans in MR08, the bivalve *Ostrea* sp. and gastropods in P204 and the polychaete *Sabellaria spinulosa*. and bivalves in P213 (Fig. 7).

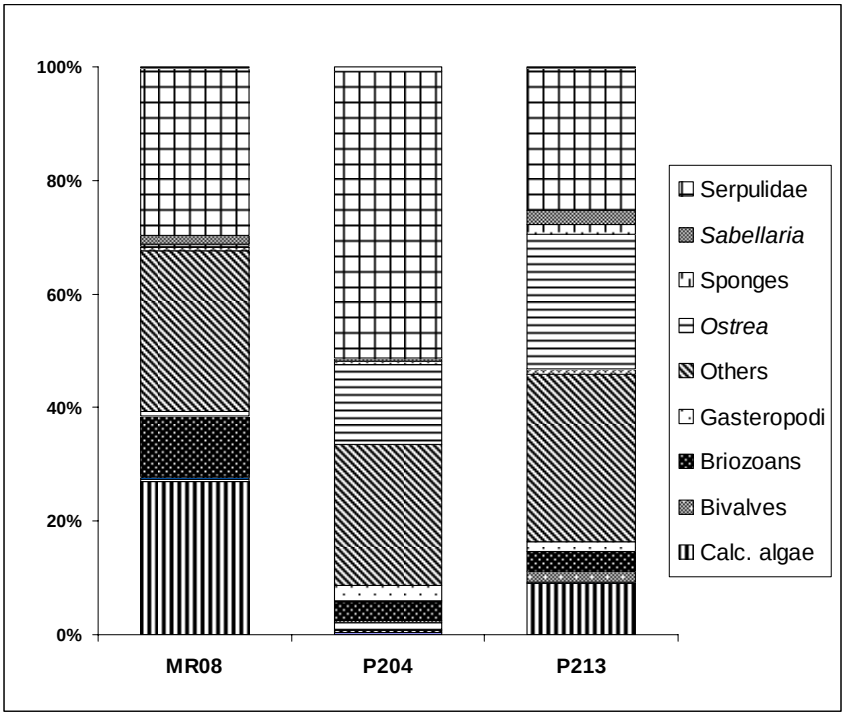


Figure 7. Bioconstruction epibionts percent contribution.

The total bioconstruction-erosion net balance in these coralligenous habitats varied only at local scale (PERMANOVA: Pl(Si) $P < 0.0001$) and the overall mean value was 212 (± 56 e.s.) $g_{AM}\ m^{-2}\ y^{-1}$ (Fig. 8).

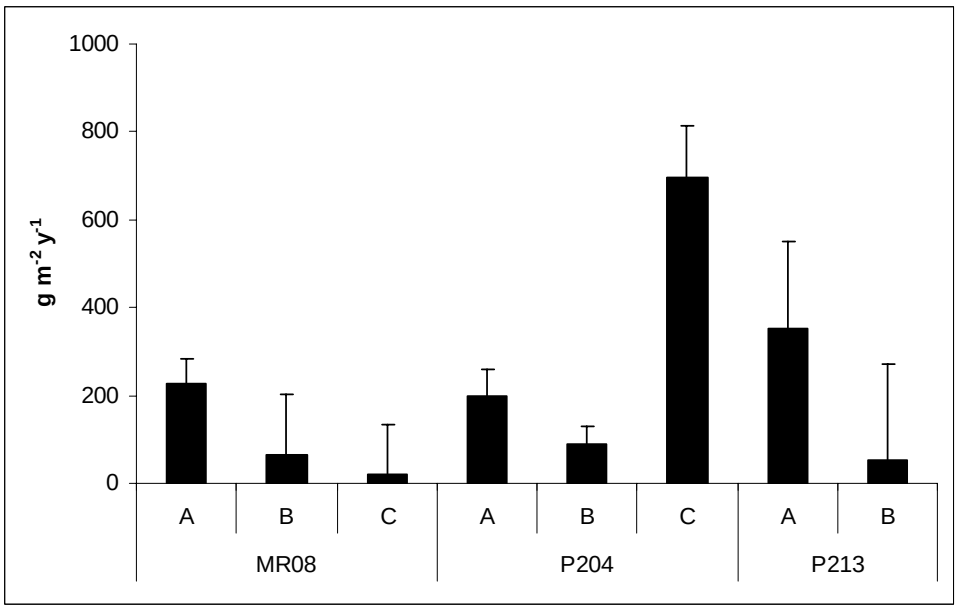


Figure 8. Bioconstruction-erosion net balance (mean value ± e.s.).

Biomass

The epibenthic assemblages biomasses (g_{AFDM} $tile^{-1}$) varied among plots and sites (PERMANOVA: Pl(Si) $P < 0.001$, Si $P < 0.01$). The major contributors were calcareous algae in MR08, serpulid polychaetes in P204 and the bivalve *Ostrea* sp. in P213. In comparison with the pattern highlighted in the bioconstruction analysis, several new taxa gained in importance in term of biomass, in particular sponges and ascidians in MR08 and non calcareous algae and algal turf in P204 (Fig. 9). The total amount of biomass in the habitat didn't vary either between sites and plots.

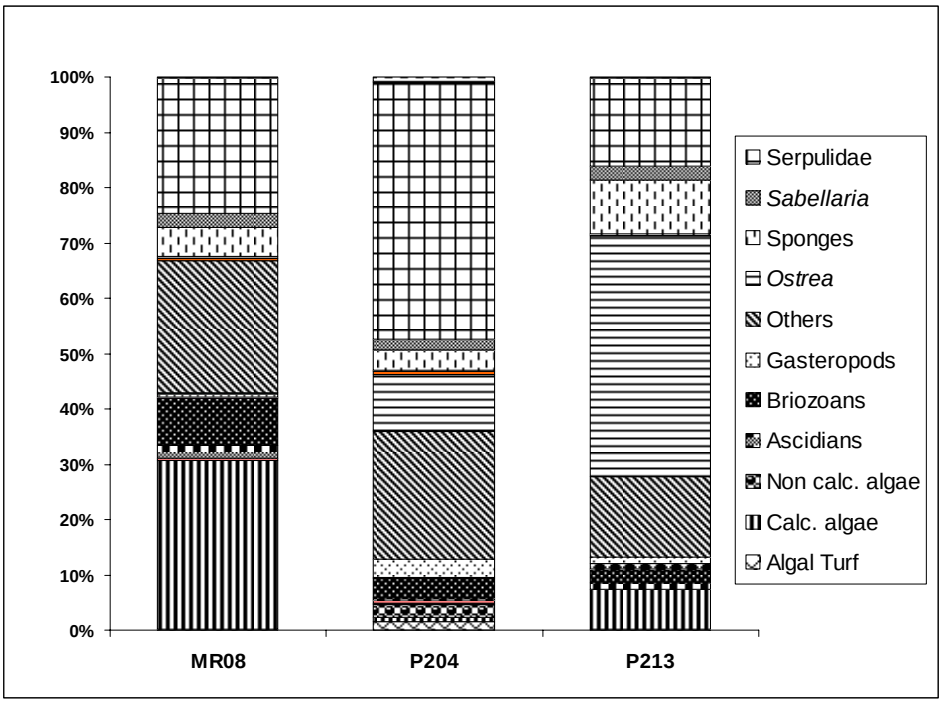


Figure 9. Biomass epibionts percent contribution

Correlation between the percent cover of the most abundant sessile specie with their biomasses were reported in Tab. 1. The conversion factors between the percent cover and corresponding biomass, calculated for the most abundant sessile taxonomic groups (i.e. calcareous algae, bryozoans, serpulid polychaetes, ascidians, algal turf), could be particularly useful to estimate the biomass and the energetic contents of the benthic assemblages starting from non-destructive photo samples.

Table 1. Linear regression ($y_{AFDM} = B\ x_{\%}$) between percent cover and biomasses ($g_{AFDM}\ m^{-2}$) of the most abundant sessile groups

Taxa	B	N	R	*P*
Calcareous algae	0.4877	24	0.750	<0.0001
Briozoans	0.1553	31	0.854	<0.0001
Serpulids	1.2958	32	0.789	<0.0001
Ascidians	0.8417	12	0.901	<0.0001
Algal turf	0.0615	17	0.873	<0.0001

Macrophytobenthos energetic content appeared heterogeneous at local scale (PERMANOVA: Pl(Si) $P < 0.01$) while that of zoobenthos didn't varied either at local or regional scale (Fig. 10). On overall the total energetic content of assemblages in these habitat didn't differed among plots and sites and its mean value was estimated in 572 (± 97.7) kJ m^{-2}.

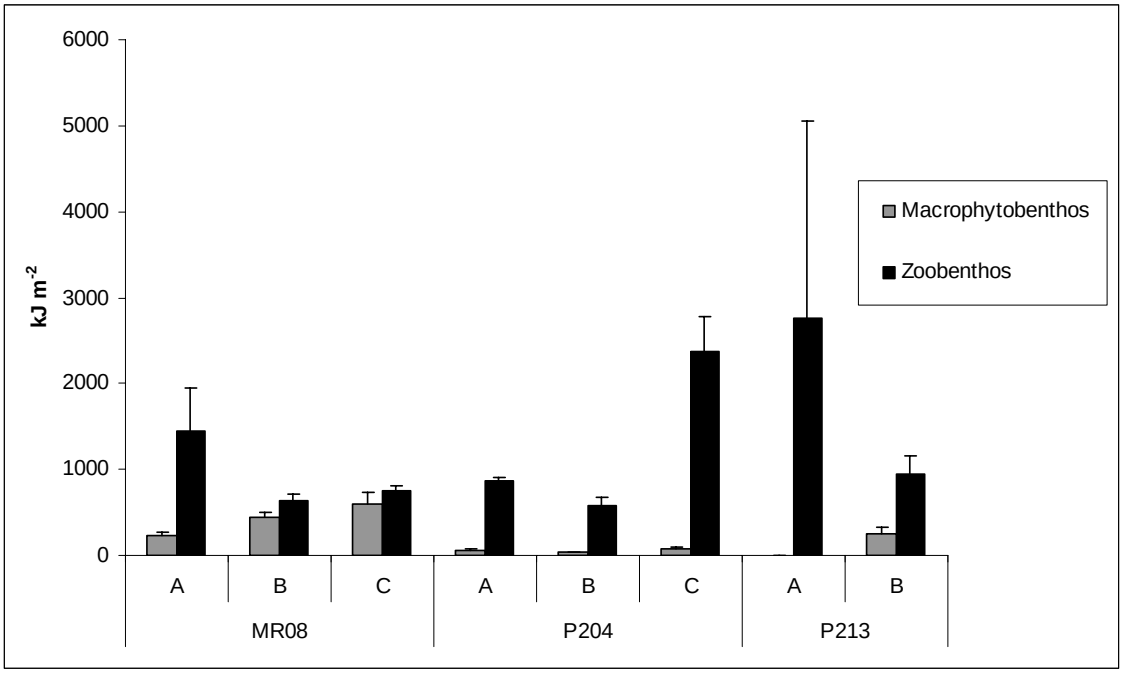


Figure 10. Macrophytobenthos and zoobenthos energetic content of epibionts (mean value ± e.s.)

Conclusion

Vagile and sessile assemblages colonising tiles over three years appeared correlated each other and significantly differed at local and regional scale. An example of vagile-sessile species interaction can be represented by the algal turf that creates a suitable environment for the gastropod *Bittium reticulatum*, which is known to be favoured by seaweed meadows (Fernandez et al. 1988). On the other hand, the abundance of *Chiton* sp. increased in calcareous-algae dominated habitat. An intimate association among a species of the grazer chiton and its primary prey, a crustose coralline alga, is well note in the Caribbean reef-building system resulting in an increased biomass and accretion of algae (Littler et al. 1995).

In the northern Adriatic coralligenous habitats, bioconstruction prevailed on erosion processes, as observed in other Mediterranean coralligenous habitats and differently from several tropical reefs where erosion processes assumes more relevance (Sartoretto 1998). The mean inorganic mass production estimated in the northern Adriatic subtidal coralligenous habitats laid in the middle of those estimated by Canals and Ballesteros (1997) in the algal-dominated (464.6 g m^{-2} y^{-1}) and animal-dominated (169.6 g m^{-2} y^{-1}) coralligenous habitats of the Mallorca-Menorca shelf. In the studied sites, the relative contribution of different taxa to the reef building did not vary among sites and the inorganic mass production was largely attributed to serpulid polychaetes rather than to calcareous algae. The importance of serpulid polychaetes in develops and maintains the marine biogenic construction was already pointed out in other subtidal Mediterranean habitats (Laborel 1987; Cocito 2004). Although the benthic sessile and vagile assemblages largely differed between sites, confirming previous evidences (Ponti et al. 2011), the net bioconstruction rates didn't vary among them. This suggests the existence of a potential construction occurring at all sites, regardless of the composition of the

assemblages, probably dependent to the homogenous spatial distribution of reef builder organisms at regional scale.

While the main builder organisms were similar at all sites, the site-specific taxa contribution to the assemblage biomasses is very variable. Beside the high biomass supported by calcareous species, contributions to the total biomass come also from non-calcareous species like ascidians and algal turf and some vagile species, which varied significantly among sites. Despite this variability, the mean total biomass was the same at each plot and site. Similarly, total energetic content of the benthic assemblages did not vary among sites. The presence of the same total energy content in the benthic communities at all sites, despite this being provided by different species, suggests the achievement of a carrying capacity of the system, may determined by trophic flows. Ultimately, both bioconstruction processes and energetic storage seems to be limited by the resources availability.

The phytobenthos energetic contribution was mainly attributed to calcareous algae and appeared lower than that of zoobenthos, owing to the large amount of filter feeders in these habitats. This demonstrates how planktonic food web primarily supports the energy flow in these benthic habitats. This is in accordance to the high phytoplanktonic primary production, as well to the high water turbidity and the reduced irradiance reaching the bottom in the northern Adriatic continental shelf (Bernardi Aubry et al. 2004).

Short note. Effect of thermal stress on the zooxanthellate temperate octocoral *Maasella edwarsi* (De Lacaze-Duthiers, 1888)

Introduction

Maasella edwarsi (De Lacaze-Duthiers 1888) is one of the few Mediterranean zooxanthellate soft corals. It consists of groups of polyps connected by stolons, which can be overgrown by calcareous red algae (Weinberg 1977).

These animals occur on hard substrates from 12 m (Viguier 1888) to 40 m (Laubier 1966) and probably deeper (Berenguier 1954). As described by Parenzan (1977) *Maasella edwarsi* had been recorded in Banyuls sur Mer ({De Lacaze-Duthiers 1888 #44150}, 1900; Laubier 1966), in Alberes (Laubier 1966), in Marseilles (Berenguier 1954), in Naples (Von Koch 1891) and in Algeria (Viguier 1888; De Lacaze-Duthiers 1888, 1900). Along the Italian coast, it has been sighted in the Tyrrhenian, Ionian and Adriatic sea (Morri et al. 2008; Fava and Ponti 2007; see also some recent shallow water reports in Sardinia and Croatia by http://www.reefcheckitalia.it/). On the 26 northern Adriatic subtidal rocky outcrops investigated by Ponti et al. (2001), *M. edwarsi* was found only at one site, where it presented a dense population widespread over an area of about 100 m^2 (Fava and Ponti 2007). Little is known about its reproductive cycle except for the note of Motz-Kossowska (Motz-Kossowska and Fage 1907), who described this species as gonocoric, and the spawning events observed by Viguier (Viguier 1888), Lo Bianco (Lo Bianco 1909) and Fava and Ponti (2007).

The little known biology, the fragmented distribution of locally dense populations, and the symbiosis with zooxanthellae, make this species particularly interesting. Its singular distribution on the northern Adriatic biogenic outcrops could be related to some environmental conditions (i.e. light, temperature, salinity, sedimentation rate, etc.) that are involved in structuring and maintaining the species diversity of these coralligenous

assemblages (Ponti et al. 2011). The increased frequency of the summer thermocline deepening, due to climatic anomalies and the consequent thermal stress, raise questions on the possible future scenario of the distribution of *M. edwarsi*. The possible responses to increasing temperature were analysed by some preliminary experiments in laboratory.

Materials and Methods

Colonies of *Maasella edwarsi* were collected in a northern Adriatic rocky outcrop (45° 12.269' N 12° 24,351' E) located offshore Chioggia at 21 m in depth. The colonies were gently removed from rocky surface, preserved in refrigerated and oxygenated seawater during the transport and then kept in thermostat aquaria. Soft coral colonies were placed into sixteen 200 ml glass beakers filled with 100 ml of 1 μm filtered seawater. Eight beakers were maintained at 18°C, the same temperature recorded on the sea bottom during the sampling, while others eight were exposed to 24°C, as recorded on the bottom during a summer thermal anomaly. The beakers were illuminated with 15W deep sea fluorescent tubes (380-450 nm), delivering 0.9 μmol photons m^{-2} s^{-1} on a 12/12h light/dark cycle and maintained with a constant salinity of 38 ‰. Each beaker was oxygenated by aerator and covered with Parafilm to prevent evaporation. After three and six days, some polyps were removed with scissor from each beaker and homogenized in a blender with 1 μm filtered seawater. A portion was preserved with formalin for later zooxanthellae counts and another aliquot was used for chlorophyll measurement. The chlorophyll (Chl) a and c2 concentrations were determined after overnight extraction in 90% acetone and absorbance readings at 664 and 630 nm according to Jeffrey and Humphrey (1975). The concentration of zooxanthellae within colonies tissues was obtaining using a Neubauer haemocytometer under a light

microscope. Both zooxanthellae and chlorophyll density measures were normalised to the wet mass of sampled polyps. Mean chlorophyll (a + c2) content in the zooxanthellae was calculated by dividing the chlorophyll by the number of zooxanthellae measured for the same sample (Winters et al. 2009).

Differences among treatment (Tr: 2 levels, fixed: 18°C, 24°C) and time (Ti: 2 levels, fixed: 3 days, 6 days) were tested using a distance-based two-way permutational analysis of variance (PERMANOVA; Anderson and ter Braak 2003). Univariate analyses were based on the Euclidean distances of untransformed data. The relation between zooxanthellae density inside polyps and chlorophyll concentration of both polyps and zooxanthellae were estimated by linear regression. The probability that the fitting line slope differed from zero was investigated by ANOVA.

Results

Colonies exposed to higher temperature showed a significant lower concentration of chlorophyll a + c2 in comparison with those maintained in natural condition, independently by the time elapsed (PERMANOVA: Tr $p<0.05$) ((Fig. 1)

Similarly the concentration of zooxanthellae varied among the two different thermal treatment, in particular colonies stressed with high temperature hosted a lower amount of symbionts (PERMANOVA: Tr $p<0.05$) (Fig. 2).

Correlation between the density of zooxanthellae vs the concentration of Chl a + c2 per both, fresh colonies mass and single zooxanthellae, had been investigated. As increased the density of zooxanthellae the total chlorophyll concentration raised (Fig. 3) while the mean chlorophyll concentration per zooxanthella reduced (Fig. 4).

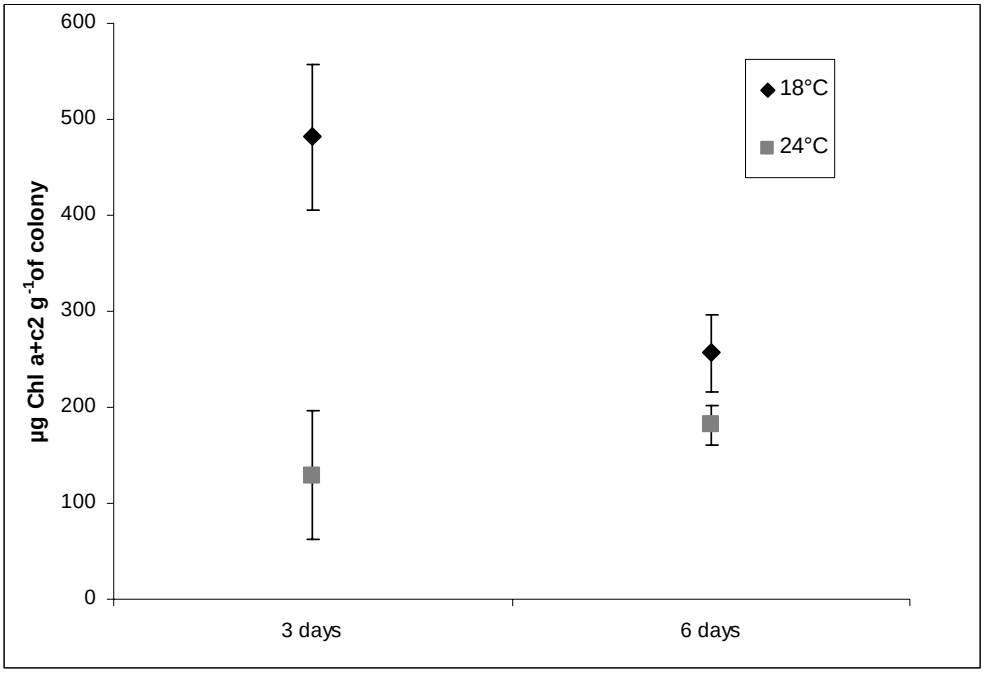


Figure 1 Concentration of chlorophyll a + c2 in relation to the exposed temperature.

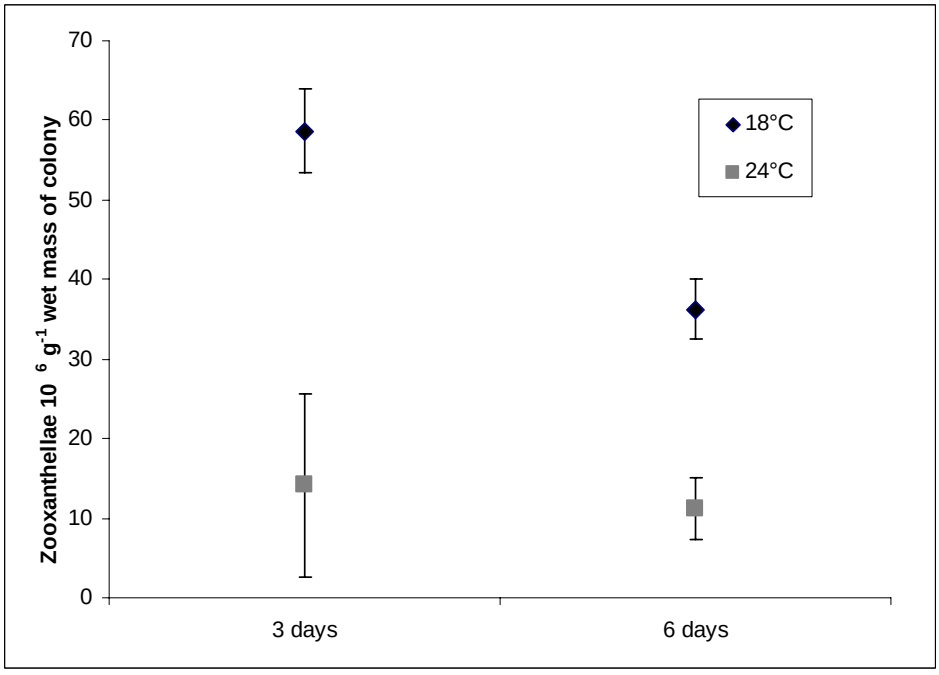


Figure 2 Concentration of zooxanthellae over time in relation to thermal treatment.

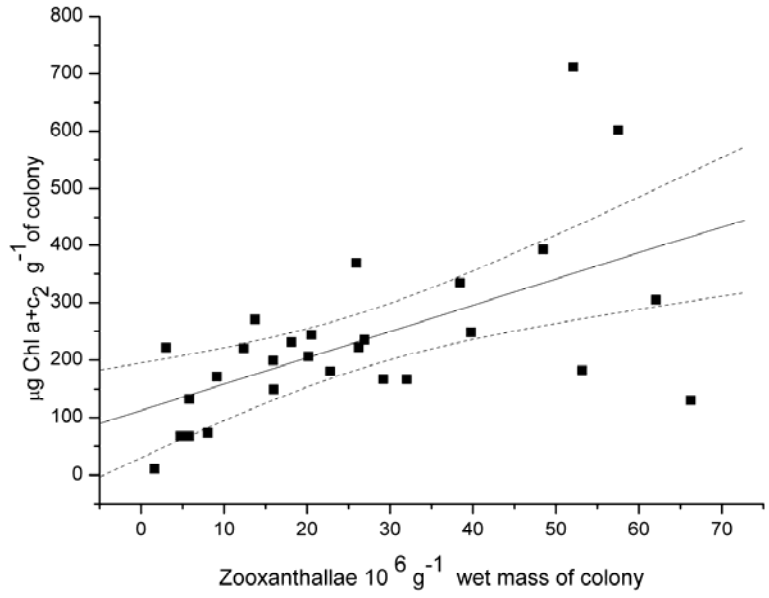


Figure 3 Zooxanthellae density vs Chlorophyill concentration per wet mass of *M. edwarsi.*

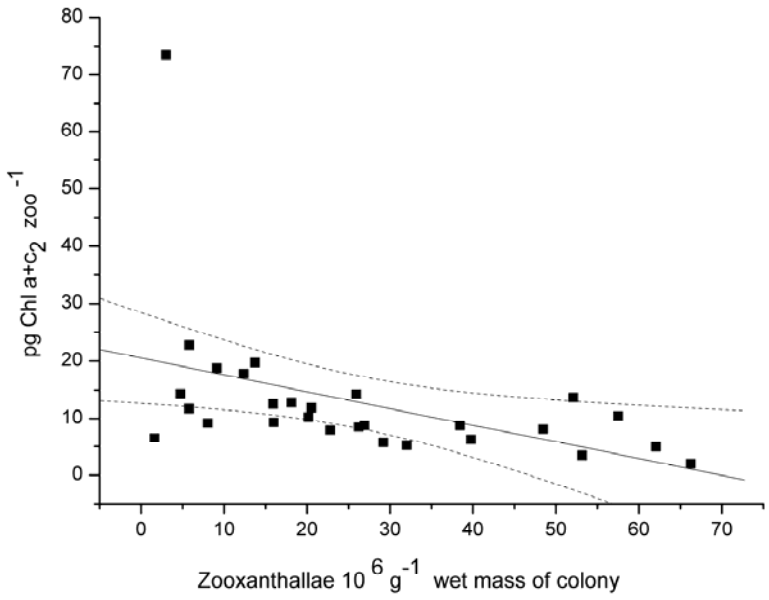


Figure 4 Zooxanthellae density vs chlorophyill a + c_2 concentration per zooxanthellae.

Table 1. Linear regression between zooxanthellae density and chlorophyill concentration per g of *M. edwarsi* and chlorophyill concentration per zooxanthellae: zooxanthellae density ($g_{\text{colony wet mass}}$) = A + B x

x	A	B	N	R	*P*
Chl zoo^{-1}	112.44	4.57	28	0.58	<0.01
Chl g $Maasella^{-1}$	20.54	-0.29	28	-0.43	<0.05

Conclusion

Increased seawater temperature has been advocated as the main stress factors in the recent large-scale bleaching events (Fitt et al. 1993, Williams and Bunkley-Williams 1990). During bleaching the symbiosis between the coral host and its symbiotic dinoflagellates (zooxanthellae) is disrupted resulting in loss of zooxanthellae and photosynthetic pigments within the algal partner (Michalek-Wagner and Wills 2001).

Maasella edwarsi represented one of the few zooxanthellate octocorals of the Mediterranean Sea, in comparison to the large amount of tropical species in which the thermal stress responses has been largely studied.

The stress response of *M. edwarsi* to increased temperature could be used to monitor seasonal thermal anomalies at local scale. Prolonged and frequent warming events could lead to a reduction of its geographical distribution. Improving the analysis on the response of temperate species to environmental alterations should be very important in relation to global climate change.

Chapter 3. General Discussion

This thesis integrates the results of three studies addressing the structure and dynamics of the epibenthic assemblages on the coralligenous subtidal reefs occurring in the northern Adriatic Sea. Until now, these assemblages were poorly documented, despite their potential importance in the ecological processes of the northern Adriatic Sea. This thesis aims at improving the knowledge on these coralligenous habitats providing informations on species composition and variability of the epibenthic assemblages and the ecological processes controlling their development.

This first regional-scale study documented the high spatial-temporal variability of these epibenthic assemblages, with a spatial variation larger compared to temporal changes. These patterns suggest that reef-forming organisms are temporally persistent and assemblages spatially varied in relation to morphological features and geographical location of the outcrops, together with variation in the hydrological conditions. The natural variability of these systems could limit our ability to detect the effect of any natural or anthropogenic disturbance event, and to predict their ecological dynamics. Understanding the patterns and causes of variability is a focal point for the management and protection of these marine habitats. Manipulative experiments help to understand the ecological processes structuring the benthic assemblages and maintaining their diversity. A short and long term experiment on colonization patterns of artificial substrata over a 3-year period has been done. Species assemblages differed among sites from the early stage of colonisation. Spatial diversification of the assemblages increased trough time and similarity with the surrounding natural assemblages progressively raised. The first colonisers, affected by the different larval supply, played a key role in determining the heterogeneity of the assemblages in the early stage of colonisation.

Lateral invasion, from the surrounding assemblages, was the driver in structuring the mature assemblages. The complex colonisation dynamics of the coralligenous habitats may contribute to explain the heterogeneity of the assemblages dwelling on the northern Adriatic biogenic reefs.

Biogenic structures are highly dynamic due to the interplay between the bioconstruction and erosion processes. The analysis of the bioconstruction-erosion balance, experimentally measured in the field, showed that bioconstruction, largely due to serpulid polychaetes, prevailed on erosion processes. Despite the large spatial heterogeneity of the sessile and vagile assemblages of the reefs, the net bioconstruction rates did not vary significantly among the single reefs. Bio-construction occurred at similar rates in all sites, probably due to the homogenous spatial distribution of reef builder organisms at regional scale. Similarly, the total energy content in the benthic communities do not differ among sites, despite being provided by different species. These results suggest the attainment of the maximum energy flow available that could represent the carrying capacity of this system. Therefore we can hypothesise that both bioconstruction processes and energetic storage may be limited by the availability of resources. The major contribution of the zoobenthos compared to the phytobenthos to the total energetic content of assemblages suggests that the energy flow in these benthic habitats is primarily supported by planktonic food web trough the filter feeding invertebrates.

In the final section of the thesis, the response to thermal stress of the soft coral *Maasella edwarsi,* a temperate zooxanthellate species forming a dense population in only one northern Adriatic reef, has been preliminarily investigated. The heat stress led to the loss of algal endosymbionts and also of pigments within algae. This may compromise the health of the animal as this association could allows both the removal of wastes

from octocoral and the translocation of photosynthetic products to the animal, fulfilling most of the host's energy demands (Muscatine 1990).

The reduction of the distribution of this species could be useful to detect the global warming effects. The increased frequency of the climate anomalies, and the consequent thermal stress, raise questions about the possible response of several species, highlighting the importance of improving study about species responses to environmental changes.

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Appendix. Publication on Marine Biology (Uncorrected proof of the 1st manuscript)

Mar Biol
DOI 10.1007/s00227-011-1661-3

ORIGINAL PAPER

Spatial–temporal variability of epibenthic assemblages on subtidal biogenic reefs in the northern Adriatic Sea

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Received: 29 July 2010 / Accepted: 25 February 2011

Abstract Spatial distribution and temporal variation of epibenthic assemblages of coralligenous biogenic rocky outcrops occurring in the northern Adriatic Sea (45°24′–45°04′N; 12°23′–12°43′E) were investigated by photographic sampling from 2003 to 2006 at 12 randomly selected sites. The dominant reef-forming organisms were the encrusting calcareous algae (*Lithophyllum stictaeforme*, *Lithothamnion minervae* and *Peyssonnelia polymorpha*), while the main bioeroders were boring sponges (*Cliona viridis*, *C. celata*, *C. thoosina*, *C. rhodensis*, *Piona vastifica*) and the bivalve *Gastrochaena dubia*. Composition of the assemblages varied thorough years and among sites. Spatial heterogeneity, at local and regional scale, prevailed over temporal variation. This variability was related both to the geo-morphological features of the outcrops and to environmental variables. Sites clearly differed in the per cent cover of reef builder and bioeroder species while only limited temporal variation within site was found. Some taxa revealed complex intra-site temporal trends. These results provide valuable information on the diversity and variability of epibenthic assemblages of the northern Adriatic coralligenous reefs, essential for the management and conservation of these unique biogenic habitats.

Introduction

Mediterranean coralligenous concretions are biogenic reefs formed mainly by the accumulation of calcareous encrusting algae growing in dim light conditions (*sensu* Ballesteros 2006). Their structure is shaped by the growth patterns of dominant algal species, together with lithification and erosion processes. Coralligenous reefs occur between 20 and 120 m in depth along the Mediterranean coast (Laborel 1987). Coralligenous rims grow on coastal rocks (e.g. vertical cliffs, overhangs and outer part of marine caves), while platform banks develop on the continental shelves over consolidated sediments, coalesced rhodoliths or pre-existing rocky outcrops (Laborel 1987). The latter generally presents biogenic flat reefs with a thickness varying from 0.5 to 4 m, often surrounded by sedimentary bottoms (Ballesteros 2006). Coralligenous assemblages include algal and animal builders, bioeroders, several epi- and endo-faunal species; moreover, they host a rich cryptofauna (Hong 1982). These habitats are considered a "hot spot" of species diversity in the Mediterranean sea (Boudouresque 2004); therefore, these reefs are intrinsically valuable for their biological diversity and for the ecological processes that they can support (Ballesteros 2006). Mediterranean coralligenous assemblages are threatened by several sources of human disturbance (e.g. pollution, sediment deposition, recreational fishing and trawling, diving) (Hong 1983; Garrabou et al. 1998; Airoldi 2003 and reference therein; Balata et al. 2005). Global environmental changes, leading to mass mortality events (Cerrano et al. 2000; Linares et al. 2005; Garrabou et al. 2009) and invasions by alien species (Occhipinti-Ambrogi 2007; Piazzi and Balata 2009), are an additional source of disturbance to these habitats. Other important causes of mortality for these benthic assemblages are bottom

Communicated by F. Bulleri.

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Journal : Large 227 | Dispatch : 4-3-2011 | Pages : 13
Article No. : 1661 | ☐ LE | ☐ TYPESET
MS Code : MABI-D-10-00375 | ☑ CP | ☑ DISK

hypoxia/anoxia events (Ott 1992; Kollmann and Stachowitsch 2001; Zuschin and Stachowitsch 2009 and references therein), and suffocation by mucilaginous aggregates (Molin et al. 1992; Russo et al. 2005 and references therein). Both phenomena periodically happen in the northern Adriatic Sea.

Conservation and management of the Mediterranean coralligenous habitats require quantifying patterns of variability of the benthic assemblages at a range of spatial and temporal scales (Garrabou et al. 1998; Ferdeghini et al. 2000; Piazzi et al. 2002, 2004; Balata et al. 2006; Virgilio et al. 2006). Several studies have recently investigated spatial variability of coralligenous assemblages on coastal rocky cliffs, while structure and variability of platform banks have been rarely investigated.

Although northern Adriatic platform banks were firstly mentioned in the 18th century (Olivi 1792), to date, their benthic assemblages has been analysed only in few locations (Brunetti 1994; Gabriele et al. 1999; Mizzan 2000; Molin et al. 2003; Soresi et al. 2004) and their spatial and temporal variability remains little known (Fava et al. 2009a, b). An approximate checklist of the benthic organisms living on these outcrops can be found in Casellato and Stefanon (2008).

The aim of this study was to investigate spatial and temporal variability of the species assemblages on the coralligenous reefs of the northern Adriatic platform at regional-scale throughout 4 years. Moreover, possible correlations of the species assemblages with environmental variables, geo-morphological features and habitat complexity, were investigated.

Materials and methods

Study area

Coralligenous biogenic reefs of the northern Adriatic continental shelf range from a few to several thousands square metres in size, and up to 4 m in height from surrounding bottoms (Newton and Stefanon 1975). In the present study, 26 coralligenous reefs, locally named 'tegnùe', scattered over an area of about 500 km^2, at a depth ranging between 18 and 30 m, and distant 6–24 km from the coast, were investigated (Fig. 1). Each outcrop was labelled in accordance with previous publications (e.g. Ponti and Mescalchin 2008; Fava et al. 2009a). The sedimentary bottoms surrounding the outcrops were mainly characterized by terrigenous sediments superimposed to the Würmian glaciation continental deposits (10–7,000 years ago; Trincardi et al. 1994). Sea currents in the area are driven by the cyclonic geostrophic circulation and by its summertime baroclinic component (Artegiani et al. 1997a, b). A strong seasonal halocline and thermocline are found in the area; light penetration to the bottom was strongly affected by fluvial runoff, current transport of sediments and phytoplankton blooms (Bernardi Aubry et al. 2004 and references therein). Measures taken in two stations at 25 m in depth indicated an irradiance of about 30–150 MJ m^{-2} year^{-1} (Franco 1984), corresponding to a light attenuation of 1–2% of the mean surface irradiance, estimated in 5,800 MJ m^{-2} year^{-1} (Bernardi Aubry et al. 2004).

Sampling and laboratory analyses

Composition and abundances of the epibenthic assemblages were investigated annually, using a non-destructive photographic sampling method, on 12 randomly selected sites located on separated rocky outcrops some kilometres apart (Fig. 1, Table 1). Photographic samples (17.0 × 22.6 cm, 0.0384 m^2) were collected from 2003 to 2006 in August, using an Olympus Cammedia C-7070 WZ underwater digital camera (7 Mpixel) equipped with a TTL strobe and two 50-Watt halogen lights. A rigid spacer connected to the camera guaranteed constant distance and parallelism between focal plane and substrata. Ten random photoquadrates were analysed at each sites for each sampling date. This photographic method could underestimate the abundance of some species, like the coralline algae, sometimes partially hidden by other organisms, but it has been widely used in study dealing with spatial and temporal variability of hard bottoms epibenthic assemblages because it allowed large-scale high replicated investigations (Bianchi et al. 2004). Sampling area and number of replicates were defined based on the size of the species occurring on the outcrops and in accordance with the methodologies commonly used on the Mediterranean hard bottoms (Bianchi et al. 2004). Species reference collection over the 26 investigated outcrops (Fig. 1) was created by collecting voucher specimens, corresponding to field photographs collection, to allow the identification of the organisms to the lowest possible taxonomic level. Per cent cover of sessile organisms was quantified by superimposing a grid of 100 equal-sized squares and identifying all taxa visible within each quarter of these squares, i.e. ±0.25% (Meese and Tomich 1992; Dethier et al. 1993). Per cent cover was related to the total readable area of each image, obtained subtracting dark and blurred zone or portion covered by motile organisms. Organisms were identified in accordance with the species reference collection and assigned to morphological and ecological groups. The endolithic bioeroder bivalve *Gastrochaena dubia* was identified and quantified by counting the siphon holes.

Location and morphology of each sampling site was obtained by DGPS and single beam sonar survey, which allowed the 3D GIS-based mapping. Habitat complexity

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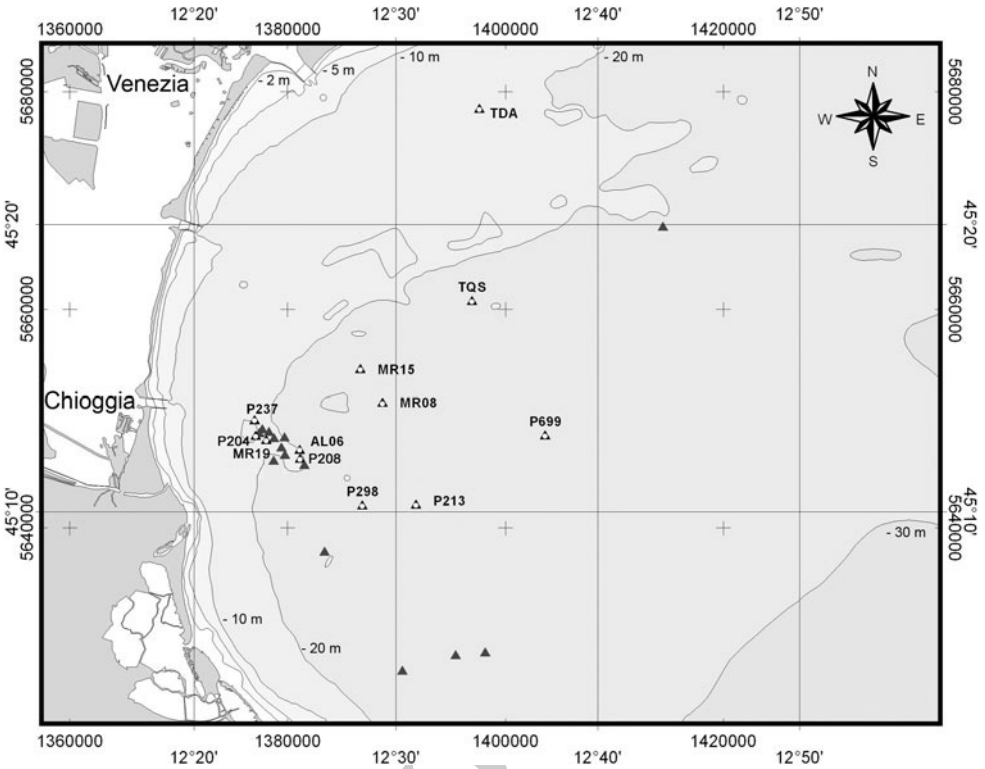

Fig. 1 Map of study area, showing the explored rocky outcrops and the twelve randomly selected sampling sites (projection grid utm33 wgs84)

Table 1 Location (geographical coordinates, datum wgs84), geo-morphological features (depth, distance from the coast, extent and height of relief, habitat complexity), surrounding sediment and water characteristics (mud (i.e. silt + clay), organic matter, mean temperature and salinity) of the study sites

Site	Lat N	Lon E	Depth (m)	Coast dist. (km)	Extent (m^2)	Height (m)	Habitat complexity	Mud (%)	Organic matter (% LOI)	Mean T Aug °C	Mean T (Jun–Aug) °C	Mean S (Jun–Aug) (psu)
AL06	45° 12.188′	12° 25.258′	21.9	8.5	27,759	2.1	109.98	26.48	4.46	24.11	21.63	37.79
MR08	45° 13.831′	12° 29.354′	22.2	14.6	2,096	1.5	64.13	7.76	4.98	23.54	21.18	37.90
MR15	45° 14.978′	12° 28.258′	23.3	13.6	400	1.5	29.74	22.54	3.24	23.88	21.42	37.84
MR19	45° 12.519′	12° 23.598′	21.1	7.0	441,917	1.5	120.59	22.1	6.06	24.88	22.46	37.52
P204	45° 12.674′	12° 23.076′	20.2	6.6	276,297	2.2	234.54	38.79	4.46	24.88	22.45	37.52
P208	45° 11.877′	12° 25.260′	23.0	8.3	2,380	1.5	49.35	19.91	4.53	24.11	21.62	37.80
P213	45° 10.270′	12° 31.013′	25.4	15.0	1,288	1.2	44.70	19.37	1.82	23.09	20.86	37.95
P237	45° 13.218′	12° 23.020′	20.7	6.8	9,634	4.2	154.30	48.15	4.82	25.07	22.68	37.44
P298	45° 10.240′	12° 28.354′	24.3	11.5	489	0.8	18.47	32.34	3.34	23.02	20.74	37.98
P699	45° 12.683′	12° 37.406′	27.0	23.9	900	0.8	12.45	21.84	4.63	22.24	20.25	38.05
TDA	45° 24.040′	12° 34.150′	19.4	7.5	1,600	3.7	153.18	6.98	5.94	25.17	22.94	37.39
TQS	45° 17.355′	12° 33.792′	23.4	19.5	375	0.8	15.93	24.59	3.65	24.21	21.66	37.81

(Hci) was estimated linearly combining the rugosity index, height and extent of relief. The rugosity index was estimated as mean ratio between the contoured and straight length among two points (Brokovich et al. 2006) on a 10-m cross-section of the outcrop carried out from the digital bathymetries, replicated six times for each site.

Sediment samples were collected close to the outcrops. Sand and silt–clay content was measured as dry weight percentage after wet sieving (0.063 mm mesh), retaining the fine fraction by filter paper (particle retention 11 μm), and drying at 90°C for 24 h. Sediment organic content was determined as per cent loss of weight of the dried samples at 90°C for 24 h, after ignition (*% LOI*) at 500°C for 8 h (King et al. 1998).

Hydrographical data were not available for the area, mean daily temperature (°C) and salinity (psu) near the bottom at each sampling site and for the whole study period were estimated using the ASHELF model. ASHELF is a

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numeric model developed within the ADRICOSM project (http://gnoo.bo.ingv.it/adricosm/), based on the Princeton Ocean Model (Zavatarelli and Pinardi 2003 and references therein) with data assimilation for the northern Adriatic basin with a 1.5 km grid.

Data analyses

Epibenthic assemblages were analysed in terms of per cent cover. Species richness (number of taxa, *S*), species diversity (as Hill's diversity number $N1 = \text{Exp}\ H'$, where H' is the Shannon's index) and the corresponding evenness component (as $N10 = N1/S$) were calculated for each replicate sample (Gray 2000). Two-way analysis of variance (ANOVA) was applied to single taxon and to diversity indices to test for differences among years (4 levels, random) and sites (12 levels, random). The homogeneity of variances was assessed by Cochran's C test, and data were transformed if required. Only when data were distinctly binomially distributed, the arc-sin transformation was applied (Underwood 1997). Percentages of variance components (VC%) were calculated in order to estimate the magnitude of the variability attributable to spatial and temporal factors in comparison with the residual variations among replicates (Underwood 1997).

Spatial distribution and temporal variation of the assemblages were analysed using both principal coordinate analysis (PCO, i.e. metric multidimensional scaling) and cluster analysis (complete linkage method) based on Bray-Curtis similarity of square root transformed data (Gower 1966; Clarke 1993). Each sampling site was represented on the PCO bi-dimensional ordination plot by the centroid of 10 replicates. Distance-based two-way permutational multivariate analysis of variance (PERMANOVA; Anderson 2001; Anderson and ter Braak 2003) was used to test for differences of epibenthic assemblages among the investigated years (4 levels, random) and sites (12 levels, random). The analysis was based on Bray-Curtis dissimilarities on squared root transformed data. Percentages of variance component (VC%) were calculated for each terms of the analysis.

Relationship between the similarity patterns of the assemblages and environmental variables were investigated by multivariate multiple regression using the DISTLM forward procedure that provided a selection of variables that better explain the observed patterns (McArdle and Anderson 2001). The selected environmental variables were extent (Log_{10} transformed) and height of relief, depth, habitat complexity, distance from coast, longitude and latitude (UTM33 wgs84 coordinates), sediment mud (% silt + % clay) and organic matter (% *LOI*) content in the surrounding seabed, mean bottom temperature and salinity in August and during the summer (June–August) each year.

Possible linear correlations among the most abundant species per cent cover and diversity indices with the environmental variables that better explain the assemblage's similarity patterns have been investigated by linear regression. The probability that the fitting line slope differed from zero was investigated by ANOVA.

Results

Flora and fauna

The epibenthic assemblages found on the investigated northern Adriatic coralligenous reefs were very heterogeneous in terms of per cent cover of the most abundant taxa. The assemblages were characterized by algal turf (per cent cover between 2.7 and 61.37%), calcareous red algae (0.2–52.35%), encrusting sponges (0.07–20.28%), massive sponges (0.07–25.31%), boring sponges (0–25.44%), colonial ascidians (0–18.23%), tubular sponges (0–9.5%) and zoantharians (0–22.8%).

The dominant reef-forming organisms were encrusting calcareous red algae that mostly consisted of *Lithophyllum stictaeformae* (Areschoug in J. Agardh) Hauck, 1978, *Lithothamnion minervae* Basso, 1995 and *Peyssonnelia polymorpha* (Zanardini) F. Schmitz, 1879, while other uncalcified red algae included *Halymenia floresii* (Clemente y Rubio) C. Agardh, 1817 and *Botryocladia botryoides* (Wulfen) Feldmann, 1941. Algal turf was mainly composed by the Rodophyta *Polysiphonia* sp., *Antithamnion* sp. and *Rhodymenia* sp. and by the Chlorophyta *Cladophora* sp. and *Chaetomorpha* sp. The main bioeroders were the boring sponges *Cliona celata* Grant,1826, *Cliona rhodensis* Rützler & Bromley, 1981, *Cliona thoosina* Topsent, 1887, *Cliona viridis* (Schmidt, 1862), *Pione vastifica* (Hancock, 1849) and the endolithic bivalve *Gastrochaena dubia* (Pennant, 1777). In terms of trophic guilds, epibenthic invertebrates included filter feeders, among which the most common were the sponges *Antho* (*Antho*) *inconstans* (Topsent, 1925), *Dictyonella incisa* (Schmidt, 1880), *Dysidea avara* (Schmidt, 1862), *Phorbas fictitius* (Bowerbank, 1866), *Mycale* (*Mycale*) *massa* (Schmidt, 1862), *Tedania* (*Tedania*) *anhelans* (Lieberkühn, 1859), the zoantharian *Epizoanthus* spp. and the ascidian *Polycitor adriaticus* (Drasche, 1883). The most common species are described in Ponti and Mescalchin (2008). The species checklist included 14 new records for the northern Adriatic Sea (see "Appendix").

Species spatial distribution and temporal variability

Overall, the per cent cover of calcareous algae (Fig. 2a), boring sponges (Fig. 2b), massive sponges, cnidarians and

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colonial ascidians showed clear spatial distribution patterns with significant differences among sites, while these groups appeared quite steady in time (ANOVA Site: $P < 0.01$; Table 2). The magnitudes of the variability among sites were similar or lower than the residual variations among replicates, indicating a high heterogeneity at local spatial scale. The abundance of non-calcareous algae (including algal turf), algal turf (Fig. 2c) and encrusting sponges showed complex site-specific temporal trends. Their differences among sites varied annually (ANOVA year × site: $P < 0.01$; Table 2), even if most of the observed variability was associated with the differences among sites and replicates.

Analysing the most abundant epibenthic species individually, the per cent cover of the calcareous algae *Lithothamnion minervae* did not vary in time but differed among sites, dominating the deepest locations (Table 3). Most of the variability of *L. minervae* was due to variations among replicates, rather than to the difference among sites.

The abundance of the encrusting sponges *Dictyonella incisa* and *Antho* (*Antho*) *incostans* differed among sites. The first sponge exhibited a slightly decreasing temporal trend and appeared abundant in shallower and wider outcrops near the coast (Table 3); the second showed a higher

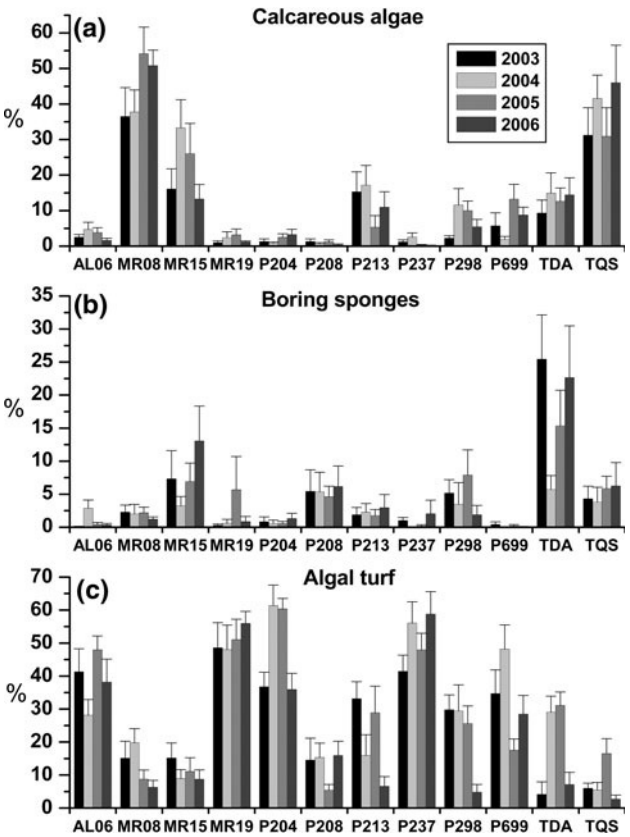

Fig. 2 Spatial and temporal trends of some ecological group: **a** calcareous algae, **b** boring sponges, **c** algal turf (mean values ± SE)

Table 2 Results from ANOVA on epibenthic per cent cover data of the most important ecological groups (VC% = percentage of variance components)

Source	*df*	Calcareous algae				Non-calcareous algae				Algal turf				Encrusting sponges				*F* ver.
		MS	*F*	*P*	VC%	MS	*F*	*P*	VC%	MS	*F*	*P*	VC%	MS	*F*	*P*	VC%	
Year (Y)	3	5.595	1.83	0.1611	0.39	1149.230	1.09	0.3671	0.13	1522.647	1.76	0.1748	0.96	2.514	0.63	0.5991	0.00	Y × S
Site (S)	11	118.556	38.75	0.0000	53.09	12083.890	11.46	0.0000	44.38	10785.860	12.44	0.0000	43.55	25.511	6.42	0.0000	18.18	Y × S
Y × S	33	3.060	1.24	0.1751	1.08	1054.716	3.97	0.0000	12.69	867.067	3.40	0.0000	10.75	3.972	1.76	0.0065	5.81	RES
Res	432	2.471			45.44	265.949			42.80	254.752			44.74	2.251			76.01	
Transf.		Sqrt($X + 1$)				None				None				Sqrt($X + 1$)				
Source	*df*	Boring sponges				Massive sponges				Cnidarians				Colonial ascidians				*F* ver.
		MS	*F*	*P*	VC%	MS	*F*	*P*	VC%	MS	*F*	*P*	VC%	MS	*F*	*P*	VC%	
Year (Y)	3	1.305	1.56	0.2171	0.30	7.374	2.79	0.0559	1.17	0.902	1.19	0.3275	0.14	0.336	0.26	0.8518	0.00	Y × S
Site (S)	11	13.547	16.22	0.0000	24.28	33.474	12.66	0.0000	22.83	10.793	14.27	0.0000	29.56	12.909	10.08	0.0000	22.89	Y × S
Y × S	33	0.835	0.85	0.7135	0.00	2.644	1.03	0.4196	0.25	0.756	1.31	0.1241	2.09	1.280	1.35	0.0955	2.63	RES
Res	432	0.987			75.42	2.558			75.75	0.579			68.21	0.946			74.48	
Transf.		Ln($x + 1$)				Sqrt($X + 1$)				Ln($X + 1$)				Ln($X + 1$)				

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Table 3 Results from ANOVA on epibenthic per cent cover data of the most abundant species (VC% = percentage of variance components)

Source	*df*	*Lithothamnion minervae*				*Dictyonella incisa*				*Antho incostans*				*F* ver.
		MS	*F*	*P*	VC%	MS	*F*	*P*	VC%	MS	*F*	*P*	VC%	
Year (Y)	3	667.936	2.46	0.0804	0.00	2.731	3.22	0.0353	1.29	4.246	3.09	0.0402	1.96	Y × S
Site (S)	11	8842.842	8.87	0.0000	0.35	21.482	25.29	0.0000	42.30	10.113	7.37	0.0000	17.93	Y × S
Y × S	33	2991.503	0.95	0.5558	0.00	0.849	1.27	0.1513	1.47	1.373	1.47	0.0472	3.62	RES
Res	432	41380.990	2.46		99.65	0.670			54.94	0.932			76.48	
Transf.		ArcSin(%)				Ln(x + 1)				Ln(x + 1)				
Source	*df*	*Cliona viridis*				*Gastrochaena dubia*				*Polycitor adriaticus*				*F* ver.
		MS	*F*	*P*	VC%	MS	*F*	*P*	VC%	MS	*F*	*P*	VC%	
Year (Y)	3	1.596	1.67	0.1914	0.42	36.306	15.2	0.0000	19.26	0.323	0.31	0.8203	0.00	Y × S
Site (S)	11	13.562	14.24	0.0000	24.77	13.016	5.45	0.0001	18.11	11.963	11.35	0.0000	23.93	Y × S
Y × S	33	0.953	1.00	0.4693	0.01	2.388	3.16	0.0000	11.12	1.054	1.25	0.1694	1.83	RES
Res	432	0.952			74.80	0.756			51.51	0.846			74.24	
Transf.		Ln(x + 1)				Ln(x + 1)				Ln(x + 1)				

spatial–temporal heterogeneity and a general increasing trend with depth (Table 3). The boring sponge *Cliona viridis* showed a site-specific distribution with a high abundance in some small outcrops, in particular in the site TDA, located off the Venice town (Table 3). The colonial ascidian *Polycitor adriaticus* was characterized by not significant variation among years and by high spatial heterogeneity with higher abundance in small and deep outcrops far from the coast (Table 3). These four species showed most of their variability associated with the sites and to the variation among replicates, indicating a greater importance of spatial variability compared to the temporal changes.

The abundance of the endolithic bivalve *Gastrochaena dubia* showed an extremely high variability in both space and time (Table 3).

Species richness (*S*), species diversity (*N1*) and evenness (*N10*) showed high significant differences in the interaction year × sites confirming the great spatial and temporal heterogeneity of the assemblages (Table 4). In particular, at all sites the number of species seemed to follow a common decreasing temporal trend during the first 2 years, and a subsequent increase.

Spatial–temporal variability of the epibenthic assemblages

Epibenthic assemblages showed a high variability in terms of both space and time, as showed by the PCO ordination plot (Fig. 3a). The first two axes of the PCO explained 44.4 and 12.0% of the variability of epibenthic assemblages, respectively. The scatter plot discriminated the assemblages inhabiting different sites, as confirmed by PERMANOVA showing significant interaction between year and site (Table 5). In addition, variability among sites was greater compared to the temporal changes as showed by the percentages of the variance components (Table 5). The cluster analysis detected five main groups of assemblages represented by: (1) four outcrops located near the shore (AL06, MR19, P204, P237); (2) three small outcrops quite far from the coast (MR08, MR15, TQS); (3) three south-eastern outcrops (P213, P298, P699) and the site TDA in August 2004 and 2005; (4) the site TDA in August 2003 and 2006; (5) the site P208 alone (Fig. 3a). These clusters seemed to reflect the geographical position of the outcrops. Similarity of the assemblages among years within each site was generally higher than the similarity among sites in the

Table 4 Results from ANOVA on species diversity indices (VC% = percentage of variance components)

Source	*df*	*S*				*N1*				*N10*				*F* ver.
		MS	*F*	*P*	VC%	MS	*F*	*P*	VC%	MS	*F*	*P*	VC%	
Year (Y)	3	48.424	5.19	0.0048	7.25	2.852	0.700	0.5615	0.00	0.154	4.71	0.0076	3.96	Y × S
Site (S)	11	32.287	3.46	0.0028	12.78	19.835	4.840	0.0002	18.50	0.195	5.95	0.0000	15.91	Y × S
Y × S	33	9.329	3.16	0.0000	14.19	4.102	2.790	0.0000	12.39	0.033	1.70	0.0101	5.50	RES
Res	432	2.954			65.77	1.469			69.11	0.019			74.63	
Transf.		None				None				None				

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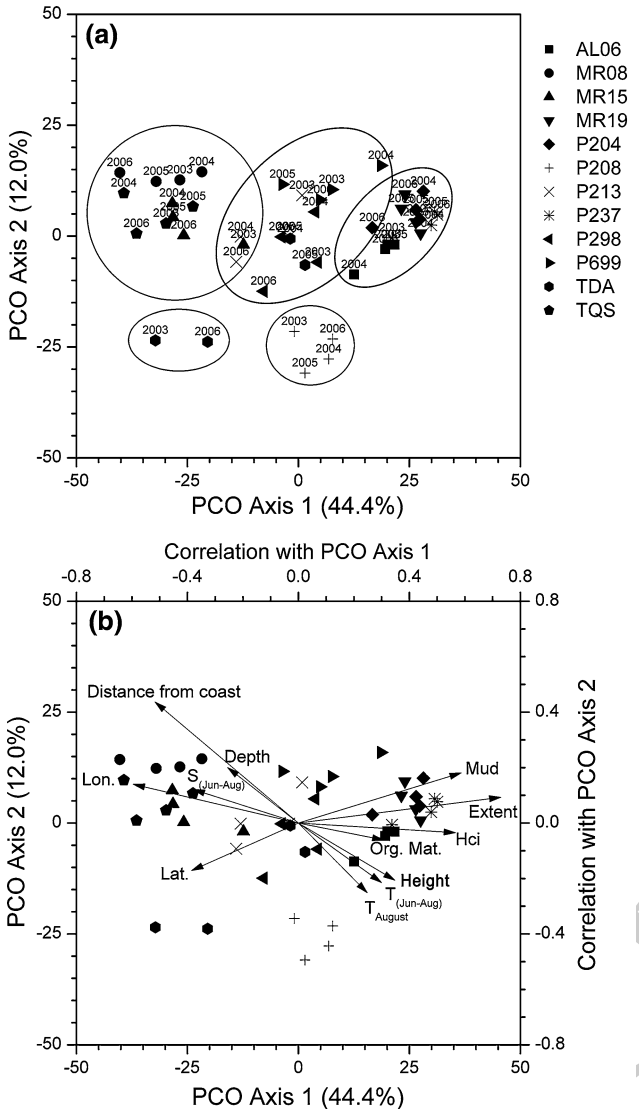

Fig. 3 PCO unconstrained ordination plot (i.e. metric MDS) based on Bray-Curtis dissimilarities of square rout-transformed epibenthic assemblages per cent cover data: **a** *symbols* represent sampling sites, while years are indicated by *numbers*, *lines* show clusters obtained at an arbitrary similarity level of 55%; **b** correlation of environmental variable with PCO Axes, represented by superimposed vectors

Table 5 Results from PERMANOVA on Bray-Curtis dissimilarities of square rout-transformed epibenthic per cent cover data (VC% = percentage of variance components)

Source	*df*	SS	MS	Pseudo-F	*P* (perm)	Unique perms	VC%
Year (Y)	3	35,886	11,962	3.2911	0.0001	9,876	2.64
Site (S)	11	358,100	32,555	8.9567	0.0001	9,850	27.51
Y × S	33	119,950	3634.7	2.2224	0.0001	9,655	7.61
Res	432	706,530	1635.5				62.24
Total	479	1,220,500					

same year; therefore, patterns of similarity were driven by spatial rather than temporal variability (Fig. 3a).

Correlation between epibenthic assemblages and environmental variables

Vectors superimposed on the PCO plot graphically represented the relationships between environmental variables and patterns of similarity of the epibenthic assemblages (Fig. 3b). Multivariate multiple regressions indicated that the environmental variables were significantly correlated with the patterns of similarity of the benthic assemblages (Table 6). In particular, the cluster of assemblages located near the coast was related to an increase of mud, sediment organic matter, extent and height of relief and summer seawater temperature, while assemblages far from the shore were related to depth and summer salinity.

Abundance of algal turf and the encrusting sponge *Dictyonella incisa* significantly increased with the extent and height of the outcrops as well as with mud and organic matter content of nearby sediment, while it decreased with the distance from the coast, longitude and salinity (Table 7). On the contrary, *Lithophyllum stictaeforme*, *Lithothamnion minervae*, *Cliona viridis* and *Polycitor adriaticus* were particularly abundant at sites far from the coast and were negative correlated with mud sediment content and outcrops extent (Table 7). These results are in agreement with the features of the near shore outcrops, which were generally wider, more elevated from the surrounding bottoms, strongly influenced by fluvial inputs, water temperature and salinity.

Species richness and diversity increased with depth and salinity and decreased with habitat complexity, height of

Table 6 Multivariate multiple regression (DISTLM forward procedure) between epibenthic assemblages similarity pattern and environmental variable

Variable	SS(trace)	Pseudo-F	*P*	Prop.	Cumul.
Extent (Log10) of relief	12,923	15.4530	0.0002	0.2515	0.2515
Distance from coast	4,882	7.2833	0.0002	0.0950	0.3465
Depth	4,093	5.3576	0.0002	0.0796	0.4261
Height of relief	3,612	6.0013	0.0002	0.0703	0.4964
Longitude	2,332	4.1580	0.0002	0.0454	0.5418
Mud (% silt + clay)	2,056	3.9218	0.0002	0.0400	0.5818
Temp. in August	1,825	4.0867	0.0002	0.0355	0.6173
Organic matter (% LOI)	1,375	2.7330	0.0022	0.0267	0.6440
Mean temp. (June–August)	1,323	2.7457	0.0018	0.0257	0.6698
Mean salinity (June–August)	1,227	2.8843	0.0010	0.0239	0.6937
Habitat complexity	1,212	3.2537	0.0006	0.0236	0.7172
Latitude	1,028	2.5135	0.0046	0.0200	0.7372

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Table 7 Correlation matrix displaying *r* values among selected taxa, groups of taxa, diversity indices and habitat complexity with environmental variables

	Extent of relief (Log_{10})	Depth	Height of relief	Habitat complexity	Distance from coast	Longitude	Latitude	Mud (% clay + silt)	Org. Matter (%LOI)	Temperature in August	Mean temp. (June–August)	Mean Sal. (June–August)
Lithophyllum stictaeforme	−0.452**	0.199	−0.366*	−0.446***	0.537***	0.359*	0.150	−0.302*	−0.146	−0.247	−0.298*	0.330*
Lithothamnion minervae	−0.502***	0.095	−0.106	−0.257	0.323*	0.563***	0.454***	−0.511***	−0.243	-0.166	−0.093	0.119
Cliona viridis	−0.389**	−0.287*	0.214	−0.041	−0.126	0.331*	0.722***	−0.516***	0.122	0.232	0.230	−0.136
Antho (Antho) inconstans	−0.001	0.443**	−0.314*	−0.128	0.170	0.089	−0.445**	0.070	−0.272	−0.415**	−0.323*	0.278
Dictyonella incisa	0.729***	−0.480***	0.466***	0.580***	−0.634***	−0.739***	−0.245	0.635***	0.385**	0.564***	0.516***	−0.483***
Tedania anhelans	−0.444**	0.309*	−0.316*	−0.425**	0.395**	0.266	0.038	−0.252	−0.511***	−0.239	−0.249	0.366**
Epizoanthus arenaceus	0.011	−0.053	0.042	−0.058	−0.329*	−0.248	−0.106	−0.098	0.095	0.132	0.135	−0.143
Polycitor adriaticus	−0.513***	−0.003	−0.089	−0.302*	0.298*	0.461***	0.448***	−0.422**	−0.146	0.009	−0.038	0.115
Calcareous algae	−0.513***	0.150	−0.308*	−0.416**	0.525***	0.484***	0.311*	−0.414**	−0.162	−0.227	−0.236	0.294*
Algal turf	0.698***	−0.258	0.316*	0.552***	−0.374**	−0.476***	−0.296*	0.551***	0.312*	0.190	0.263	−0.381**
Boring sponge	−0.075	0.261	−0.365*	−0.313*	0.427**	0.219	−0.010	0.026	−0.224	−0.087	−0.144	0.194
Colonial ascidians	−0.558***	0.076	−0.169	−0.389**	0.373**	0.488***	0.419**	−0.465***	−0.154	−0.052	−0.131	0.161
S	−0.244	0.415**	−0.429**	−0.371**	0.218	0.084	−0.383**	−0.131	−0.419**	−0.481***	−0.556***	0.608***
N1	−0.520***	0.338*	−0.350*	−0.514***	0.241	0.270	−0.056	−0.342*	−0.223	−0.377**	−0.445**	0.469***
N10	−0.649***	0.345*	−0.329*	−0.537***	0.375**	0.498***	0.225	−0.514***	−0.260	−0.204	−0.233	0.154

*** $P < 0.001$; ** $P < 0.01$; * $P < 0.05$

relief, water temperature and organic and mud content in the nearby sediment respectively (Table 7).

Discussion

The epibenthic assemblages of coralligenous outcrops were mainly composed, in terms of per cent cover, by algal turf, calcareous algae and sponges. Results highlighted the importance and the structural role of macroalgal species (Curiel et al. 2010) that has been largely neglected by previous researches (Casellato et al. 2007; Gabriele et al. 1999). Similarly, sponges' richness has been largely disregarded (5 taxa in Gabriele et al. 1999, 13 in Molin et al. 2003, 27 in Casellato et al. 2007). In the present study, 40 different species of sponges were found, including 8 new records for the Italian coast of the northern Adriatic Sea.

Distribution and abundance of the epibenthic assemblages among the investigated outcrops differed thorough years and sites, with a spatial heterogeneity being larger than temporal changes. This pattern of variation was confirmed by the distribution of the most abundant taxa (e.g. *Cliona viridis*, *Lithothamnion minervae*, *Polycitor adriaticus*), which varied among sites but were largely consistent in time. These patterns indicated a great temporal persistence of the organisms that characterize the coralligenous communities, as also observed by Garrabou et al. (2002) in north-western Mediterranean coralligenous assemblages. Temporal fluctuations were mostly evident for non-reef-forming organisms as algal turf and other non-calcareous algae.

The environmental factors in a heterogeneous system as coralligenous habitat could greatly change at local and geographical scale; therefore, their influence is little known and hard to quantify (Ballesteros 2006). Irradiance and sedimentation rate on the investigated outcrops can vary with their distance from coast and depth. Moreover, near shore outcrops were generally wider and more elevated from the surrounding bottoms. Morphological features and geographical location of the outcrops affected the spatial distribution of the assemblages, while hydrological conditions that changed over time were less relevant.

The irradiance values on sea bottom in the study area (Franco 1984) were comparable to those recorded in coralligenous concretions developed on horizontal surfaces in other Mediterranean continental shallow coastal waters (i.e. Tossa de Mar; Ballesteros 2006). Light availability in the study area decreased approaching the coast because of the presence of several fluvial inflows that deeply affect turbidity, sediment and nutrients supply and phytoplankton growth. Therefore, distance from the coast and river mouths could be included among the drivers of the spatial variability observed in the northern Adriatic epibenthic assemblages. As a result, algal turf was more abundant in the sites near the coast with high mud and organic matter contents in the surrounding bottoms. On the contrary, the calcareous algae *Lithophyllum stictaeforme*, *Lithothamnion minervae* and the erect sponge *Tedania anhelans* were positively correlated with distance from the coast and negatively correlated with mud contents in the surrounding bottoms. These patterns can be explained by the higher resistance to sedimentation and turbidity of algal turf compared to erect and encrusting organisms. Algal turf are known to be able to spread very quickly by vegetative reproduction, independently by the stress regime (Airoldi 1998; Gorgula and Connell 2004; Balata et al. 2005).

Habitat complexity could affect the distribution and abundance of some species, as well as species diversity (Archambault and Bourget 1996 and references therein). Morphologically complex habitat has been shown to be normally associated with a greater species richness (Bergeron and Bourget 1986; Johnson et al. 2003). These observations are in contrast with the present results that showed a negative correlation between habitat complexity and species richness and diversity. The relation between habitat complexity and diversity could be affected by the spatial scale considered here, as habitats could appear homogenous or heterogeneous depending on the spatial scale of observation (Kolasa and Rollo 1991). In the studied area, the most morphologically complex outcrops were located near the shore, where algal turf monopolized space under high sediment deposition, reducing local spatial scale species diversity.

Mediterranean coralligenous habitat showed large spatial and temporal variability at multiple scales. Natural variability of this system could alter our ability to detect the effect of any natural or anthropogenic disturbance event and to predict their ecological processes (Denny et al. 2004). In order to protect and manage this marine environment, comprehension of patterns and causes of its variability become a focal point. This regional-scale study provides information on the spatial–temporal variability of epibenthic assemblages and on the distribution pattern of the main organisms. This knowledge could be useful to develop effective growing indicators and ecological status indices for the northern Adriatic coralligenous outcrops based on the ratio between reef builders and bioeroders. The possible effects of some environmental factors have been underlined, but further correlative and manipulative studies should be done to investigate the specific role of these factors.

Acknowledgments This study is part of the PhD thesis of F. F. We would like to acknowledge Marco Bertolino, Carlo Cerrano, Francesco Mastrototaro, Guido Bressan for their taxonomic help, Marco Zavattarelli and Luca Giacomelli for oceanographic data, Andrea Pasteris for statistical support, and the no profit association "Associazione Tegnùe" for the logistic support. We also thank two anonymous reviewers for their useful comments.

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Appendix

See Table 8.

Table 8 Epibenthic sessile flora and fauna reference collection (* new records for the northern Adriatic Sea)

Class	Family	Species
Florideophyceae	Halymeniaceae	*Halymenia floresii* (Clemente y Rubio) C. Agardh, 1817
		* *Halymenia latifolia* P.L. Crouan & H.M. Crouan ex Kützing, 1866
	Rhodymeniaceae	*Botryocladia botryoides* (Wulfen) Feldmann, 1941
	Peyssonneliaceae	*Peyssonnelia polymorpha* (Zanardini) F. Schmitz, 1879
	Corallinaceae	* *Lithothamnion minervae* Basso, 1995
		Lithophyllum stictaeforme (Areschoug in J. Agardh) Hauck, 1978
Ulvophyceae	Ulvaceae	*Ulva laetevirens* Areschoug, 1854
Demospongiae	Plakinidae	*Oscarella lobularis* (Schmidt, 1862)
	Geodiidae	*Geodia cydonium* Jamenson, 1811
	Clionaidae	*Cliona celata* Grant,1826
		Cliona rhodensis Rützler & Bromley, 1981
		Cliona viridis Schmidt, 1862
		* *Cliona thoosina* Topsent, 1887
		Pione vastifica (Hancock, 1849)
	Tethydae	*Tethya aurantium* (Pallas, 1766)
	Polymastiidae	*Polymastia mamillaris* (Müller, 1806)
	Suberitidae	* *Pseudosuberites sulphureus* (Bean in Bowerbank, 1866)
		Suberites domuncula (Olivi, 1792)
	Chondrillidae	*Chondrosia reniformis* Nardo, 1847
	Microcionidae	* *Antho* (*Antho*) *inconstans* (Topsent, 1925)
	Coelosphaeridae	*Lissodendroryx* (*Lissodendroryx*) *isodictyalis* (Carter, 1882)
	Microcionidae	*Clathria* (*Clathria*) *compressa* (Schmidt, 1862)
	Hymedesmiidae	*Phorbas tenacior* (Topsent, 1925)
		Phorbas fictitius Bowerbank, 1866
	Tedaniidae	*Tedania* (*Tedania*) *anhelans* Lieberkühn, 1849
	Myxillidae	*Myxilla* (*Myxilla*) *rosacea* (Lieberkühn, 1859)
	Esperiopsidae	* *Ulosa stuposa* Esper, 1794
	Mycalidae	*Mycale* (*Mycale*) *massa* (Schmidt, 1862)
	Axinellidae	*Axinella damicornis* (Esper, 1794)
		Axinella polypoides Schmidt, 1862
	Bubaridae	* *Bubaris vermiculata* (Bowerbank, 1866)
	Dictyonellidae	*Acanthella acuta* Schmidt, 1862
		* *Dictyonella incisa* (Schmidt, 1880)
	Agelasidae	*Agelas oroide*s Schmidt, 1864
	Chalinidae	*Haliclona* (*Haliclona*) *simulans* (Johnston, 1842)
		Haliclona (*Reniera*) *mediterranea* Griessinger, 1971
	Chalinidae	* *Haliclona* (*Soestella*) cfr. *mamillata* (Griessinger, 1971)
	Petrosidae	*Petrosia* (*Petrosia*) *ficiformis* (Poiret, 1789)
	Ircinidae	*Sarcotragus spinosulus* Schmidt, 1862
		Ircinia variabilis (Pallas, 1766)
	Spongiidae	*Spongia* (*Spongia*) *officinalis* Linné, 1759
	Dysideidae	*Dysidea fragilis* (Montagu, 1818)
		Dysidea avara (Schmidt, 1862)
	Aplysinidae	*Aplysina aerophoba* Nardo, 1843
		Aplysina cavernicola Vacelet, 1959
	Ianthellidae	*Hexadella racovitzai* Topsent, 1896

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Table 8 continued

Class	Family	Species
Hydroidomedusae	Eudendriidae	*Eudendrium* spp. Ehrenberg, 1834
	Tubulariidae	*Ectopleura crocea* (L. Agassiz, 1832)
Anthozoa	Hormathiidae	*Adamsia carciniopados* (Otto, 1823)
	Paralcyoniidae	* *Paralcyonium spinulosum* (Delle Chiaje, 1822)
		* *Maasella edwardsi* (De Lacaze-Duthiers, 1888)
	Sagartiidae	*Cereus pedunculatus* (Pennant, 1777)
	Cornulariidae	*Cornularia cornucopiae* (Pallas, 1766)
	Aiptasiidae	*Aiptasia mutabilis* (Gravenhorst, 1831)
	Caryophyllidae	*Caryophyllia smithii* Stockes e Broderip, 1828
	Faviidae	*Cladocora caespitosa* (Linnaeus, 1767)
	Dendrophylliidae	*Leptopsammia pruvoi* Lacaze-Duthiers, 1897
	Epizoathidae	*Epizoanthus* spp. Gray, 1867
	Parazoanthidae	*Parazoanthus axinellae* (Schmidt, 1862)
	Cerianthidae	*Cerianthus membranaceus* (Spallanzani, 1784)
Polychaeta	Sabellidae	*Sabella spallanzanii* (Claparède, 1868)
		Bispira spp. Krøyer, 1856
	Serpulidae	*Serpula vermicularis* Linnaeus, 1767
		Serpula concharum Largerhans 1880
		Pomatoceros triqueter (Linnaeus, 1767)
		Hydroides pseudouncinata pseudouncinata Zibrowius 1971
Polyplacophora	Chitonidae	*Chiton olivaceus* Spengler, 1797
Gastropoda (Prosobranchia)	Vermetidae	*Serpulorbis arenarius* (Linnaeus, 1767)
Bivalvia (Pteromorphia)	Anomiidae	*Anomia ephippium* Linnaeus 1758
	Arcidae	*Arca noae* Linnaeus, 1758
	Mytilidae	*Mytilus galloprovincialis* Lamark, 1819
	Pinnidae	*Pinna nobilis* Linnaeus, 1758
		Atrina pectinata (Linnaeus,1767)
	Ostreidae	*Ostrea edulis* (Linnaeus, 1758)
Bivalvia (Heterodonta)	Gastrochaenidae	*Gastrochaena dubia* (Pennant, 1777)
Gymnolaemata	Phidoloporidae	*Rhynchozoon neapolitanum* Gautier, 1962
Ascidiacea	Pycnoclavellidae	* *Pycnoclavella* cfr. *taureanensis* Brunetti, 1991
	Polycitoridae	*Cystodytes dellechiajei* (Della Valle, 1877)
		Polycitor adriaticus (Drasche, 1883)
	Polyclinidae	*Aplidium conicum* (Olivi, 1792)
		* *Aplidium tabarquensis* Ramos-Espla, 1991
		* *Aplidium* cfr. *densum* (Giard, 1872)
	Ascidiidae	*Phallusia mammillata* (Cuvier, 1815)
		Phallusia fumigata (Grube, 1864)
	Styelidae	*Styela plicata* (Lesueur, 1823)
		Botryllus schlosseri (Pallas, 1776)
	Pyuridae	*Microcosmus vulgaris* Heller, 1877
		Pyura microcosmus (Savigny, 1816)
		Ascidiella aspersa (O.F. Müller, 1776)

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